The Eye of Pecten.

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With Plates 6 and 7, and 2 Text-figs.

The first reference to the eyes of Pecten that I have been able to find is that of Poli in 1795. Since that date more than a score of investigators have studied these small organs and treated in more or less greater detail the histology. Each has made new discoveries, which have in very many cases been refuted by their immediate successors, to such an extent, in fact, that it was almost impossible to determine from the literature on the subject the truth in regard to certain parts. One of the last and most reliable papers was that of Hesse, published in 1900 (**34**). He pointed out that some points were still unsolved (though adding one or two discoveries himself), and that the success of the methylene-blue method, if attained, would possibly elucidate all.

In 1904 a paper appeared by Miss Hyde (**39**), embodying the results of a successful employment (according to the author) of the methylene-blue methods for nerve-endings in the retina, but these results were certainly not those expected by Hesse nor probably by other authors, for they stand in striking opposition to the views previously held. Whilst working at a memoir on Pecten in 1907, I came to the conclusion that this, the latest investigation of the Pecten eye, differed greatly from the preceding ones, and that only one

more confusing series of results had been added to the already existing multiplicity.

I determined therefore to make a complete study of the histology of the eye. The privilege of occupying the British Association Table at Naples enabled me to carry out this investigation on a species previously examined by most writers on the eye—Pecten jacobæus—and this was completed by a considerable stay at the Port Erin Biological Station. The results have been the discovery of several new points, the confirmation and refutation of many discoveries of different workers, and I hope the complete elucidation of the structure of the retina. It has been due to the frequency of occurrence of artefacts and the difficult histological work required for such complicated organs that the structure of these eyes has remained so long a puzzle.

By the use, however, of numerous methods it has been possible to eliminate to the greatest extent the artefacts, and incidentally the trial of so many fixatives, etc., has enabled me to obtain practically all the appearances seen and figured by the various investigators.

The account of the structure will be given at some length, since a comparison of the various views is necessary, and, with the exception of Hickson's and Patten's papers very little has appeared in English. I am indebted to the British Association for permission to use their table at the Zoological Station of Naples, and also to the staff of that well-known institution. My thanks are also due to Professor Herdman and to the Curator of the Port Erin Biological Station for the trouble taken in supplying me with material and apparatus for carrying out detailed work at the latter place, and to Professor Drew, of Maine, for specimens of P. tenuicostatus.

History.

Only the history of the references to the Pecten eye before and including the fundamental paper of Hensen will be given in this section, since the other works will be discussed more

fully when describing the structures involved, and it will avoid repetition if they be omitted here. In 1795 Poli, in his large work on the Mollusca (**1**), gave figures illustrating the general anatomy of Pecten, in which the eyes are depicted, and also a view of the mantle-edge showing more clearly the tentacles and eyes, but no details of structure are given whatever except the external pigmented ring bounding the cornea and the pigment stripe on the tentacles.

He recognised a likeness to the human eye, and as usual applied some of the names given to parts of the latter, a feature followed by his successors, who naturally recognised at once the resemblance to the vertebrate eye, which is such a striking character of the eyes of Pecten. These organs were mentioned, though left practically undescribed by succeeding naturalists. Cuvier refers to them as "globules verdâtres," and Lamarck as "tubercules oculiformes."

The next description is to be found in Robert Grant's 'Comparative Anatomy' (**2**), where reference is made to the "smooth cornea," the "iridescent choroidea," and a "small crystalline lens." Another English writer, Robert Garner (**3**), 1837, continued the work. He states that Pecten, Spondylus, and Ostrea (probably Pecten jacobæus, Ostrea jacobæus of Poli) possess "small, brilliant, emerald-like ocelli, which, from their structure, having each a minute nerve, a pupil, a pigmentum, a striated body, and a lens, and from their situation at the edge of the mantle, where alone such organs could be useful, and also placed, as in Gasteropoda, with the tentacles, must be organs of vision." There are no figures illustrating his short account. Almost simultaneously Krohn (**5**) and Grube (**4**) published descriptions of the eye. Grube described the position and number of the eyes in P. jacobæus, P. varius, and P. opercularis. Krohn gave a much more detailed account. He stated that the eye was a closed spherical vesicle containing two transparent bodies separated by a septum (he was therefore the first observer to see this structure). The hinder of these bodies he described as being of fibrous texture. Krohn was the first investigator to notice

that the nerve in the eye-stalk divided into two branches, one of which ran up to the optic vesicle, where he lost it, whilst the other passed up the side and entered the vesicle, lying on the septum.

Will (**6**) noticed the cellular structure of the lens, and Keferstein (**12**) recognised the retina in the hinder transparent body of Krohn. This brings us to Hensen's paper (**13**) published in 1865, which is the first account of the histology of the retina. Hensen divided this part of the eye into five layers:

1. First cell layer.
2. Second cell layer.
3. Rods.
4. Tapetum.
5. Pigment layer.

The cells of the first layer, which may be arranged in a single or double row, are spindle-shaped. The second layer is made up of cylindrical cells (the rod-cells), the third layer is that of the rods, and then follow two others—the tapetum (first demonstrated by Krohn), and the pigment layer.

The innervation is described as follows: The proximal branch of the optic nerve does not bore through the optic vesicle below, as Keferstein had assumed, but splits into a number of small branches which enclose the lower part of the optic vesicle, and these branches of the nerve form a plexus in the peripheral region of the retina. Apparently Hensen assumed that they were connected with his second cell-layer (the rod-cells)—"Der Zellenausläufer geht so continuirlich in den Nerven über, dass man nicht sagen kann, wo der eine anfängt und der andere aufhört."

The other nerve-branch penetrates the septum, and the fibres become connected to the cells of the first layer. Hensen, it will be seen, discovered the different groups of cells in the retina, described the nerve innervation correctly (though since he did not recognise two types of cells in the outer layer and in the rod-cell layer, this was probably more accidental than otherwise), and saw the axial fibre in the

rods—truly a marked advance in the knowledge of the eye-structure.

Technique.

This investigation of the eye has been carried out by the study of sections (paraffin and paraffin-celloidin), by maceration preparations and by the teasing of fixed material.

It is impossible to over-estimate the value of macerations in conjunction with section work, and the true shape of many cells could not have been determined without this method. For both fixation and maceration it was found that different reagents were necessary according to the cells to be studied. In the retina alone the various elements reacted very differently to fixatives and macerating fluids, and it was surprising to notice how different the preservation of the different cells might be after treatment with the same fixative.

The fixatives giving the best general fixation of all parts were Zenker's fluid and Carnoy's mixture. Zenker was used as follows: Fixation lasted for about twelve to twenty-four hours, and was followed by washing first with water and then in alcohol of gradually rising strength. Sections were made after paraffin embedding, the usual thickness being that of the rod-cells, namely 6 μ, but others were only 2 μ, and some were 10 μ thick. The stains used after Zenker were Mallory (connective-tissue stain), iron hæmatoxylin (Heidenhain), a modified Weigert, and picric acid—säurefuchsin.

Mallory's connective-tissue stain.—The sections, on slides, were stained in an aqueous solution of säurefuchsin, 0·05 per cent., for ten minutes, then rinsed quickly in water and placed in 1 per cent. solution of phosphormolybdic acid for three to five minutes. After washing in several changes of water for five to ten minutes the sections were stained in the following solution for eight to fifteen minutes:

Aqueous aniline blue (Grübler) . .	0·5 gr.
Orange G.	2·0 gr.
Oxalic acid	2·0 gr.
Water	100·0 c.c.

This was followed by a rapid washing out in water, dehydration in 90 per cent. alcohol to absolute, and mounting after xylol or origanum oil in balsam.

Iron hæmatoxylin.—The sections were mordanted for twenty-four hours in a 4 per cent. solution of iron alum washed in water, and stained in a 0·5 per cent. to 1 per cent. solution (aqueous) of hæmatoxylin for twelve to twenty-four hours. This was followed by differentiation under microscopic observation with 2 per cent. iron alum solution. Tap-water, alcohol dehydration, etc., as usual.

The modified Weigert method was only used after Zenker fixation. It was partly like that used by Schreiner (**30**), but modified in combination with Zenker.

Schreiner used a 10 per cent. alcoholic solution of hæmatoxylin (P. Mayer says that the "10 per cent." must be a misprint).

I used a 5 per cent. solution, but did not investigate the effects of a stronger nor of a 1 per cent. solution, which Mayer believes to be the one intended by Schreiner.

The sections (on slides) were placed in a 3 per cent. solution of potassium bichromate for twenty-four hours, then rinsed in water and alcohol, and placed in a 5 per cent. solution of hæmatoxylin (alcoholic) for a time varying from ten minutes to an hour. The sections must be black, and this takes place much quicker after the hæmatoxylin solution has been used once or twice and is oxidised by contamination with bichromate. After staining, the sections were rinsed in water and placed in a saturated aqueous solution of copper acetate, which turns them a steel-blue colour. Differentiation was carried out (under microscopic observation) in the following solution:

Borax	2·0 gr.
Pot. ferricyanide	2·5 gr.
Distilled water	100·0 c.c.

The sections were then washed in tap water and mounted in the usual way, after alcohols and xylol, in Canada-balsam.

Picric acid—säurefuchsin (van Gieson).—The sections

were stained in Delafield's hæmatoxylin and washed well in tap water. This was followed by staining for five minutes in a mixture of—

1 per cent. solution (aqueous) säurefuchsin .	5·0
Saturated solution of picric acid in water .	100·0

The stained sections were washed in tap-water and taken up to balsam as usual.

Carnoy's fixative was used in the following strength:

Chloroform	10·0
Acetic acid	30·0
Absolute alcohol	60·0

This is the best fixative for the retina. Iron hæmatoxylin and Bethe's toluidin blue were the stains used on material so fixed.

Bouin's fluid ('Lee,' edit. vi., p. 76) gave excellent results for rod-cells and rods, especially when followed by Mallory's stain. The axial fibre of the rods was stained better by the säurefuchsin in this method than by any other except the modified Weigert. Zenker's fluid, Mann's fluid,[1] and a mixture of equal parts of corrosive sublimate saturated aqueous solution, and Hermann's platinum-osmic fluid were useful for the lens, especially the latter.

Other fixatives used were 4 per cent. formol, corrosive sublimate (aqueous solution and solution in salt water), Mayer's picronitric mixture ('Lee and Mayer,' ed. vi, p. 68), Flemming, Von Rath's picro-platinum-osmic mixture, and treatment with pyroligneous acid. The latter did not give particularly good results. There were also special fixing and other processes connected with the following methods—Golgi's silver process (Cajal's modification), Bielschowsky-Paton silver method for neurofibrillæ (**41**), Apathy's nachvergoldung and hæmatein IA methods, Nabias' gold method, Lists' eosin method, and methylene blue processes. The latter were failures, though injection methods, staining in aqueous solutions, solutions in Pecten serum, and dusting powder over the eye were all tried. The results given by the other and more

[1] Mann, 'Physiological Histology,' p. 96 (solution d).

ordinary methods were more complete than by the complicated ones, and there was usually a far greater freedom from artefacts. There remains finally the maceration methods to be referred to. The lens-cells, with all their peculiar processes, were easily isolated after immersion of the eyes directly in a 3 per cent. solution of chloral hydrate in sea-water for about four hours. The same solution was used for the retinal cells, and the eyes were placed, as above, directly into this medium. After two hours the retina was dissected out from the eye, placed in a drop of water on a slide, and a cover-glass supported by wax feet placed above it. Gentle tapping on the cover-glass separated the elements. Chromic acid solutions in sea-water of $\frac{1}{50}$ per cent. strength gave very good results for macerations of the rod-cells and rods.

This was also used as advised by Patten after fixation of the eyes in $\frac{1}{5}$ per cent. chromic acid for five minutes.

The maceration preparations were examined unstained, and stained with picro-carmine.

The chief species examined have been Pecten maximus and P. jacobæus, with the following others: Pecten opercularis, P. varius, P. tigrinus, and P. tenuicostatus.

Position and Number of Eyes.

The eyes of Pecten occur on the mantle-edges of both valves. The mantle-edge can be said to be divisible into three folds, the periostracal fold, the ophthalmic fold, and the velum (Pl. 7, fig. 2, *V.*). All three possess tentacles, those situated on the first two being long and mobile sensory structures, well provided with sense-cells for the perception of tactile and olfactory stimuli, whilst those on the velum are short and rather immobile.

The eyes are situated on the median fold, between the periostracal groove and the base of the velum (Pl. 7, fig. 2, *Eye*), and amongst the long tentacles. Poli in 1795 noticed a certain resemblance of the eye-stalks to the tentacles, and considered them as modifications of the latter.

The number of eyes present varies considerably for the

different species, and there is, further, considerable variation among the individual members of any species.

Carrière (21) stated that those species with large eyes possessed fewer than those with small eyes; that there were always more on the upper mantle-lobe than on the lower; and that in general, large specimens had more eyes than smaller ones of the same species.

This latter sentence was an important assertion, since it implied growth and development of new eyes during life, and certainly it appeared supported by the fact that large and small eyes exist side by side.

Patten (22) also pointed out that there were more eyes present on the left valve than on the right, and that they were larger, but he disagreed with Carrière, stating that no new eyes develop after a size of 2 centimetres has been attained. Rawitz (25) found similarly more eyes on the left mantle-lobe than on the right, and agreed with Patten on the development. Schreiner (30) agrees also with reference to the number of eyes on the two mantle-lobes, but states that those of the right are not smaller than those of the left (Patten). Had Schreiner examined P. jacobæus, the chief species investigated by Patten, he would not have made this assertion. The eyes are always more numerous on the left mantle-lobe than on the right, as all observers have found. The exact relations, however, vary in different species. The eyes are situated in three groups, on each mantle-fold, one group on the anterior auricular area (two to seven eyes close together), another on the posterior auricular area, close up against the hinge-line, and the third and largest group along the ventral margin of the mantle. Spaces without eyes separate these three regions. In each series the eyes vary considerably in size. Patten (22) asserted, in fact, that a regular arrangement of small and large eyes existed, and Rawitz (25), though denying the existence of Patten's arrangement, stated that a large eye was always followed by a small one. I have examined all the species referred to by Patten and Rawitz and find no such arrange-

ment. There is a quite irregular series, and a small eye may be followed by another small one or by two large ones, or a group of large eyes may exist together. The eyes on the left mantle-lobe exceed in number those on the right, in particular in species with the most inequivalve shells (as far as the species I have examined are concerned), that is, in P. maximus and P. jacobæus, and this difference in numbers is greatest in P. jacobæus.

The eyes in this species are far less numerous on the right lobe, and are also very much smaller (Pl. 7, fig. 2) (contra Schreiner).

I believe, however, that the greater number of eyes on the left mantle-lobe is due primarily to the fact that this valve is always uppermost, and not to its shape; and if a Pecten is turned over on to the left valve, it very soon rights itself by a peculiar turning movement. Patten (**22**) connected this numerical superiority of eyes on the left valve with its position but was puzzled to see how this could be an advantage to the animal, since the eyes on the lower mantle-fold received the light direct from above, and the eyes on the upper one were apparently directed downwards.

Schreiner (**30**) also figures them as lying pointed to the ground and at an angle of 45° to the valve. If a Pecten be watched as it opens the valves, it will be seen that the eyes of the left mantle-lobe project just outside the shell, and their field of view is practically as much above the animal as that of the eyes in the right valve. The upper valve is also a little shorter than the lower one, and lies inside it when the shell is closed; the mantle lining the lower valve is retracted accordingly to a greater extent when the shell is closing. The valves of the almost equivalve species meet, however, ventrally, and the conditions appear either more favourable to the eyes of the right mantle-lobe than in P. jacobæus, or else, as will be referred to again, this form is an older and more specialised one, and the eyes have begun to degenerate in the lower valve. Some figures are appended which will give an idea of the number of eyes in the three

groups on the mantle-edge of P. opercularis and also of the individual variation in this species (the specimens were from the Irish Sea).

Length of ant.-post. diameter. of shell in cm.	Left mantle-lobe.			Right mantle-lobe.		
	Total No.	No. on ant. ear.	No. on post. ear.	Total No.	No. on ant. ear.	No. on post. ear.
7·5	59	6	4	42	0	3
6·4	50	4	6	41	0	4
5·8	48	4	4	39	0	3
3·8	37	4	5	31	2	5
6·4	54	2	5	40	0	4
5·8	50	4	4	39	1	4
4·25	44	4	5	41	2	4
5·1	52	3	6	42	2	4
5·1	52	4	5	50	2	6
5·25	45	3	4	39	2	3
5·15	54	5	5	35	1	3
5·15	53	5	6	48	3	3
5·85	55	5	5	49	3	4
7·25	58	7	5	47	2	5
4·10	59	4	5	52	1	5
5·0	55	4	3	50	2	4
7·4	51	2	4	38	1	5
5·25	61	7	7	47	4	5
4·75	55	5	6	43	1	4
4·70	54	5	5	42	1	4
5·3	62	6	9	39	1	4
4·4	51	6	5	41	1	5
4·9	57	5	5	43	1	4

It will be seen from these figures that there is no relation between the size of the animal and the number of eyes, though if the first five only had been taken the reverse would have appeared to be the case. Possibly Carrière only examined a few and chanced to get an accidental series. No one appears to have examined the very small eyes occurring with the large ones. I sectioned some of those taken from the right mantle-lobe of Pecten jacobæus and found that they agreed in every respect with the large eyes of the left lobe, all parts being represented and in the normal positions. The

only difference was in the number of cells present; they were apparently as large as usual but fewer in number. These eyes, in fact, appeared to be young ones, or rather, they had been arrested in development and had remained with the small number of component cells characteristic of young eyes, though they were just as old as the large ones.

In examining hundreds of eyes one meets some strange abnormalities, though the latter are of rather rare occurrence. In a specimen of P. opercularis two eyes were fused together so that the pupil was oval with a slight constriction indicating the boundary of the separate organs. Often the eyes appeared with very little black pigment—that is, all the eyes of a specimen, even the "iris" cells being almost unpigmented.

I never found any of the eyes completely covered with pigment as stated by Patten, nor has this feature been met with by any of his successors.

General Structure of Eye-Stalk.

The eyes are situated at the ends of short stalks (Pl. 6, fig. 1), which, as already pointed out, were considered by Poli as modified tentacles. This eye-stalk is made up of connective tissue, which is a direct continuation of that of the mantle-edge and is clothed by an epithelial layer, also a direct continuation of the pallial epithelium.

The connective tissue is more homogeneous or hyaline in appearance than that of the tentacles, and is not broken up so much by crossing muscle-fibres, which, as might be expected, are a prominent feature of the retractile tentacles. This homogeneous tissue extends also below the eye-stalk for some distance, and the transverse muscle-fibres which raise the velum are absent under the eyes, being arranged in bundles situated between these sense-organs. Large blood-spaces occur irregularly scattered in the stalk, communicating with one another and usually containing blood-corpuscles (Pl. 6, fig. 1, *Lac.*). There is, however, scarcely such a

defined space as a "Hauptader des Augenstieles" to which these lacunæ belong (Rawitz [**25**], p. 105). Neither do they always surround the nerve (Schreiner, p. 11).

Whilst the long sensory tentacles are, in the living animal, continually in motion, being retracted and again extended, and moved from side to side, the eyes are practically motionless and point fixedly in one direction only. They contract and may move away from a point of stimulation, this being rendered possible by means of muscle-fibres, which lie longitudinally arranged, near the epithelium (Pl. 6, fig. 1, *Mus.*). The latter are narrow fibres, and are not striated, as figured by Patten. Striated muscles do occur, though elsewhere, in the mantle-edge of Pecten (**45**). The muscles occur on all sides of the eye-stalk. They terminate, according to Rawitz, always at the proximal end of the optic vesicle and are never to be found higher ([**25**], p. 105). Rawitz has presumably taken the finer muscle-fibres, which do extend up to the cornea, for connective-tissue fibres. Schreiner found practically no muscles in small eyes ([**30**], p. 11), and states that in P. islandicus, where they were exceptionally well developed on the shell side, they could be traced to the entrance of the distal branch of the optic nerve. I have traced them to this point in P. maximus, but more delicate fibrils (Pl. 6, fig. 1, *M.f.*), staining quite differently from connective-tissue fibres, extend under the epithelium as far as the edge of the cornea, and are, moreover, present between the cornea and the lens (Pl. 6, fig. 1, *N. Lf.*; Pl. 7, fig. 7, *Lf.*). These are evidently the "fine smooth fibres" mentioned by Patten in contradistinction to his "long striated muscle-cells" of the lower part of the eye-stalk. These fibrils do not, however, enter into any connection with the epithelial cells bounding the cornea, and Patten's "ciliaris" does not exist. They will be referred to again when discussing the fibres situated between the lens and cornea.

Ganglion cells do not occur scattered in the connective tissue of the eye-stalk, a fact already noted by Patten's successors, who criticised his observations on this, as on other

details, somewhat severely. The epithelium covering the eye-stalk is a direct continuation of the pallial epithelium, but is modified in various regions of the eye-stalk and becomes a transparent cornea over the free pole. Below the optic vesicle the cells are small and cubical, or rather deeper than wide (Pl. 6, fig. 1). They contain no pigment here, and the nucleus is situated near the base. A distinct cuticle is present. Some little distance below the optic vesicle these cells increase in depth and at the same time begin to contain pigment. This pigment extends further down that side of the eye which is uppermost (see fig. 1, Pl. 6; the right-hand side is the shell side of the eye and also the uppermost, since it is an eye from the left valve). At the level of the middle of the optic vesicle, that is, about the plane of the septum, the epithelial cells have attained their greatest depth and are almost filled with dark pigment, occurring in the form of fine granules. The external portion of the cells is usually less thickly crowded, and if the sections are stained to bring out the nuclei it will be seen that these have moved, with the acquisition of pigment, so that they reside near the surface instead of at the basal end. The statements of Rawitz and Schreiner in regard to the colour of this pigment in the different species appear to me to be of little importance, and in any case I can hardly confirm them. The colour of the granules in Pecten jacobæus, P. maximus, and P. opercularis is dark brown, and the exact shade varies in any one species and according to fixation and preservation; moreover, the cells are completely filled in P. jacobæus, or at least those of the upper side of the eye-stalk.

Another point that may be noted here is that the increase in height of the epithelial cells opposite the optic vesicle is common to all the species I have examined, though Rawitz states that in P. jacobæus the epithelium is everywhere the same in height and figures it as such ([25], p. 106). Pecten abyssorum possesses (Schreiner) no pigment in the cells of the mantle-edge or of the eye-stalk. Patten appears to be the only one who has noticed that there is more pigment

present on the upper side of the eye-stalk, and there is really a longitudinal band present, exactly similar (though not so definite) to the one on the corresponding side of the tentacles. The pigmented area bounding the cornea was termed the "iris" by Patten. Since, however, as described above, these pigmented cells extend far down the eye-stalk on both sides, it is difficult to make any division into regions or to define a boundary. If, moreover, the physiological action of the iris were considered solely to be that of a diaphragm, keeping out oblique rays, the name might perhaps be applied, but, as Rawitz pointed out, there is no proof whatever of this area being capable of contraction with diminution of the "pupil," and since this region is not to be homologised with the vertebrate structure of the same name it is better to use the term pigment-mantle (Pl. 6, fig. 1, *P. man.*) if a special one is necessary. Patten considered that the "pupil" could be diminished to almost half its previous diameter (p. 571), but I have been unable to find any trace of this under natural conditions, nor do any other authors appear to have been more fortunate. The same writer states that on the shell side even in fully formed eyes the pigment may sometimes be absent so that a colourless fissure is left—termed by him the "choroid fissure" (p. 578). I have not seen this in any eye examined, and fail to find any references confirming the statement of its existence.

The pigmented epithelial cells pass suddenly into the transparent cells of the cornea (Pl. 6, fig. 1, *Co.*), through which is seen in the living specimen the silvery glance of the subretinal structures. In P. maximus the depth of the tall epithelial cells may decrease slightly in one or two cells, and then the next is much lower and completely free from pigment. Sometimes, however, the decrease in height takes place after the pigment becomes absent.

The nuclei take up again a central position or a position nearer the base in the corneal cells, but there are certain exceptions which will be considered later. The cells are hexagonal in surface view and are much flatter than those of

the pigment-mantle. They are usually constricted in the middle, so that they appear hour-glass-shaped in section, an intercellular space being left between them (Pl. 7, figs. 4 and 10). Externally there is a very distinct striated cuticle (Pl. 7, fig. 10, *Cut.*) which forms a hexagonal plate over the cell, and if the cornea is carefully focussed down upon from above these hexagonal plates are seen with their edges in close contact forming a definite mosaic (Pl. 7, fig. 3). If the corneal cells are now brought into focus at about the level of the nucleus, they appear still hexagonal in section though rather irregular, and the cell-walls do not touch. The spaces left between the cells on each side are crossed by numerous intercellular bridges (Pl. 7, fig. 4). I have no doubt that these are what Patten took to be interlocking processes of the cells. Carrière (**26**) was the first to discover their true nature, but asserted that Patten could not have seen them at all, since they were finer than his interlocking processes. Schreiner (**30**) stated that the intercellular spaces were filled with a prominent cement substance which, through shrinkage during fixation, caused the appearance seen by Patten, and does not mention any intercellular bridges whatever. Rawitz was also of the same opinion and does not refer to Carrière's statement (Rawitz [**25**], p. 109). I have seen them quite distinctly in the pigmented cells of the pigment-mantle as well as in the cornea, and they have the same structure in both places. There is another detail to be mentioned here which illustrates the difficulties caused by artefacts. Patten stated that the corneal cells had basal processes like the lateral ones, but which were longer and penetrated the underlying connective tissue, reaching the lens. This has been denied by all investigators since, and I had seen no traces of any such structures in hundreds of sections examined. After using the Bielschowsky-Paton silver method, however, the result figured (Pl. 7, fig. 10) was obtained. The tissues were fixed in 4 per cent. formol and lay in 1 per cent. silver nitrate solution for three weeks, which one might say was a likely method for artefacts. On the other hand, the structures

appeared well preserved and very little contraction had taken place. The processes were very definite, and had I found them by other confirming methods I should not have hesitated to describe them as actual cell processes. I have figured, however, the preparation, and prefer to leave the question of their true nature open. The type of cornea just described is that of Pecten jacobæus, P. maximus, and P. opercularis.

Rawitz ([**25**], p. 108) divides the types of cornea into three classes: (1) Cells of cornea considerably smaller than those of the pigment-mantle, ex. P. flexuosus, P. glaber, and P. opercularis; (2) cells of cornea, smaller at periphery against the pigment-mantle, but rapidly increase towards the centre, where they equal the pigment-cells in height, ex. P. jacobæus and P. varius; (3) corneal cells are as high as cells of the pigment-mantle at periphery, but increase rapidly in height towards the centre, the nucleus lying near the base, ex. P. pusio. I hardly think it advisable to make such a division, since, in the first place, the appearance often varies with the size of the eye, and it is difficult to fix a boundary between the two first groups. The corneal cells of P. jacobæus are, moreover, not equal in height to those of the pigment-mantle, though they are much higher in comparison with the same cells in P. maximus. There is, however, a well-marked division in which Pecten pusio and also P. tigrinus can be placed. The latter is figured (Pl. 7, fig. 12). In this species the corneal cells are very different from those of P. maximus. Those next to the pigment-mantle are of similar size, or smaller than the adjoining pigment-holding cells, but towards the centre the cells increase in height very considerably until they are deeper than the pigment-cells, the height of the corneal cells being double that of the latter. The cell-boundaries are not very distinct, and intercellular bridges are not to be seen. I have been unable to make out any reason for the peculiar difference in these two forms.

The connective tissue of the eye-stalk has already been

referred to; it is continued around the optic vesicle (Pl. 6, fig. 1, *Con.*) forming the inner wall of this (the outer being formed by the epithelium), and finally persists much diminished in thickness as a thin, transparent, and practically structureless layer underlying the cornea and separating this from the lens (Pl. 6, fig. 1, *Co. S.*). This is the "pseudo-cornea" of Patten, and the "innere Pellucidaschicht" of Rawitz. Nuclei are on rare occasions to be seen in it, but generally it is free from the connective-tissue fibrils and muscle-fibrillæ, which appear in that part just outside the corneal area, under the pigment-mantle (Pl. 6, fig. 1, *M. f.*). This more hyaline character is in all probability due to the fact that light rays have to pass through this layer before entering the optic vesicle.

The Lens.—The lens (Pl. 6, fig. 1, *L.*) is one of the structures that gave much trouble to the early investigators, but has lately been considered, entirely understood, and passed over somewhat lightly. Hesse made out some new and highly interesting structures, which I have been able to confirm. I find, however, that the shape of the lens-cells has been quite misunderstood, and the cells are certainly of a very peculiar nature.

The early authors could not determine the correct shape of the lens itself. Keferstein believed it to be spherical; Hensen was uncertain, but believed it to be bi-convex ([**13**], p. 222); Hickson considered it, however, as elliptical ([**18**], p. 447).

The confusion was again due to artefacts. It may be taken as definitely proved that the lens is bi-convex. The distal surface is, however, almost flat, whilst the proximal is very convex, and may appear dome-shaped. The actual degree of convexity depends largely on the contraction which has taken place in the eye during fixation, and the lens, dissected free from its limiting elements in a living specimen, probably alters in shape considerably, since it is not of very firm consistency. The lens is suspended from the subcorneal connective tissue (Pl. 6, fig. 1, *Co. S.*), against which its lesser convex surface is fastened. In surface view this face is circular and

not elliptical. Its diameter is a little greater than the cornea, since its periphery extends under the pigment-mantle for a short distance (Pl. 6, fig. 1).

The space in which the lens is suspended is bounded by the connective-tissue wall of the optic vesicle, the subcorneal extension of the same, and by the septum (Pl. 6, fig. 1, *Sep.*), a membrane separating the dioptric part of the eye from the retina. This space was regarded by Patten as a blood-space. Carrière (**21**) first saw the blood-corpuscles in this part of the eye, and Patten, though also finding them, was at a loss to account for their presence, since the retina seemed to shut off all communication with the blood-lacunæ of the eye-stalk. Rawitz appears to have found a definite vessel running on the outer surface of the optic vesicle and entering the distal part of the eye ([**25**], p. 113). Schreiner considers these corpuscles due to pathological conditions, and remarks that the three other authors named above considered them as normal ([**30**], p. 17). This is not strictly correct, since Patten stated that they might be forced into the cavity artificially by the contraction of the connective tissue through the action of reagents.

I have only found blood-corpuscles present in this space on extremely few occasions, and on one of these, when there were many, I could trace quite easily a series of spaces in the connective tissue, connecting up the lacunæ of the eye-stalk with the lens-cavity. This may of course have been an abnormal condition, and the lacunæ may have been produced artificially. These corpuscles had been forced in on the inner side of the eye, and I find no traces of Rawitz's blood-vessel on the outer side.

The blood plays an important part in the extension of the tentacles, and if a small living Pecten is watched under the microscope, the corpuscles can be traced running rapidly along the cavities of the tentacles as they are extended and back in the reverse direction as they contract. I believe their presence in the eye is due to contraction, and that they are forced there from the lacunæ of the eye-stalk.

There is no membrane covering the lens and helping it to retain its shape. Hensen and Hickson could not find such, but Patten described a "suspensory ligament," and also stated that the lens was attached to the septum by a connective-tissue ligament (P. varius). None of Patten's successors could find any suspending capsule, neither does the connective-tissue ligament exist. The lens may touch the septum (it very often appears so in sections), but this depends on the contraction during fixation, and usually the retina leaves the posterior wall of the optic vesicle and lies across the middle, coming naturally against the proximal end of the lens. Patten's connective tissue was in all probability the sheath of the distal nerve-branch (Pl. 6, fig. 1, *Op. Ds.*), which would be touching the lens and lying between this and the septum if the retina had been forced up. Patten's theories of accommodation as expressed at some length on p. 571 I cannot confirm, and they are somewhat irrational. They have not been referred to at all by his successors. He believed that the contraction of certain muscles supposed to be attached to the suspensory ligament would cause a movement of the lens towards the retina. This meant an inward movement of the septal membrane to which the lens (according to Patten) was attached. The elevation of the lens was to be brought about "by the tendency of the elastic septal membrane to return to its natural position, after the contraction of its peripheral circular fibres has relaxed the tension upon the central portion."

There is, however, no suspensory ligament nor attached muscles, and the lens is not attached to the septum. The septum, moreover, cannot move forward without taking the whole of the retina with it, and if this was the case (rather an absurdity) the recipient elements would always be the same distance behind the lens, whether it had been elevated or otherwise. Accommodation will be referred to later when discussing Hesse's theory.

The lens cells had received little attention until Hesse described them (**34**). Hensen stated that the lens consisted

of polygonal cells with thick walls. Patten described them as irregular with excentric nuclei, which appear in many cases to have disappeared from the cells near the inner surface. Rawitz described them as polygonal and membraneless with small nuclei, and Schreiner terms them "pretty large" vesicular cells, the peripheral ones flattened, with a large nucleus and no cell-membrane. The latter writer noticed that in sections of the lens some cells appeared to be without a nucleus (see Pl. 6, fig. 1), but went no further into the question.

Hesse says (**34**) the lens "besteht wie schon lange bekannt, aus zahlreichen, dicht neben einander gepackten Zellen, deren Körper sich an einander abplatten und bisweilen eigenthümliche Formen auf den Durchschnitten zeigen."

Later he adds (p. 395) ". . . da man ferner aus einem Durchschnitt auf die Gesammtgestalt der Zellen nicht schliessen kann, so ist es nicht möglich hier einen Zusammenhang zwischen Lage des Centralkörperchens und Gestalt der Zelle festzustellen." Hesse, however, did not adopt any maceration methods to solve the difficulty presented by sections. In sections through the lens, which is well preserved in formol-fixed specimens or Hermann-sublimate, the cells only rarely possess a polyhedral shape, in fact it is only here and there that they appear sharply angular. The cell contours are very distinct and appear rounded, so that there are irregular oval, pear-shaped and long band-shaped cells (Pl. 7, figs. 5 and 6). The size, too, varies considerably, and a very small, apparently non-nucleated cell may adjoin a large one. If, however, this small cell be followed through several sections, it will be found to be merely the continuation of a cell which is elongated to an extraordinary degree. The true shape of the cells was found after macerating the eye in 2½–3 per cent. chloral hydrate solution in sea-water for four to six hours. This medium preserves admirably the delicate processes of the cells, and the preparation gives the lens-cells, separated, uncontracted, and with all details of structure undamaged.

The cells vary considerably in shape. Those near the surface of the lens, particularly the proximal surface, are flattened and are strap-shaped (Pl. 7, fig. 6, *c*.), or are constricted in the middle and have two bulging ends. The length may be very considerable. The common appearance is that depicted in fig. 5 (Pl. 7). The cells are pyriform, with the cell-body drawn out into extraordinary long tapering processes many times the length of the swollen part. In addition to this, processes are often given off very abruptly from the broad end. Other cells are more rectangular, yet also with rounded contours and the same abrupt fine processes. These extensions are wedged between adjacent cells (Pl. 7, fig. 5), which fit close together, and the result is a mass of great compactness, whose components, though having the most varied shape, fit together without intercellular spaces being left between them.

It is often quite difficult to separate some of the cells in macerations. It is now quite obvious why there appears to be no nucleus in many cells in sections, for it may be at one end and the cell be so long that many sections may cut through the latter without touching the nucleus.

The cells have a very distinct membrane, and it is difficult to imagine how this could have been missed by Rawitz and Schreiner, especially after Carrière had asserted its presence. It is easier now to understand why there is no need of a lens-capsule or supporting ligament, for the soft protoplasmic cells are tied together by their processes and the superficial cells are practically converted into fibres or straps. The contour of the lens is, in fact, as even as if formed by a connective-tissue sheath or a layer of pavement epithelial cells. The cell contents are finely granular, with a slight trace of pigment, and stain intensely with eosin. The nuclei are similar in size to those of the epithelial cells, and since the lens-cells are usually somewhat larger than the latter the nuclei can hardly be termed pretty large (Schreiner), though such terms are purely arbitrary. Hesse (**34**) discovered in the lens-cells of P. jacobæus, which had been fixed in sublimate

and stained in Heidenhain's iron hæmatoxylin, a remarkable structure. In addition to the nucleus there was present a dark staining body from which delicate but very distinct fibrils radiated out to the periphery and became attached to the cell-wall. Most of them were straight, some were bent, but all went out from the one point and all could be followed to the cell membrane if their whole length lay in the section. I have found the same structures (Pl. 7, fig. 6, *b.*), not only in material fixed and stained as above but also after the following treatment:

After fixation in Hermann-sublimate mixture and staining in iron hæmatoxylin, the shape of the cells is well preserved, the contents are homogeneous or very finely granular and stain grey, the nucleus is black, and radiating fibrillæ appear distinctly in many cells though not in all. After Zenker fixation and Mallory's stain the cell contents are very granular in appearance and stained deep red, the nuclei being yellow-red, and there is just a slight trace of the fibrillæ. They are also to be made out, though not distinctly, after Bouin fixation. Von Rath's treatment caused the cell contents to appear very granular and vesicular (Pl. 7, fig. 6, *d.*) the radiating fibrillæ were often very distinct, but the central dark staining body did not look exactly like the normal centrosome of dividing cells.

This permanent centrosome (Pl. 7, fig. 6, *Cent.*), if it be such, does not appear to have any definite position, but since it cannot be made out in macerations it is almost impossible to determine its true position, for sections cut the cells in all directions. In addition to the species enumerated by Hesse I have found these structures in P. tenuicostatus, and probably they are present in all species. Hesse naturally compared these with the centrosome and astral rays which appear in cells undergoing mitotic division. Such structures have been demonstrated as persisting in the resting stages of certain cells, in pigment-cells of fishes, and more particularly in leucocytes. It has not been possible for Hesse or myself to determine any connection with cell-division. The astral

rays are very fine and remarkably definite. There are three explanations of these structures that may be given. The first and most unlikely is that they are artificial productions; the second, that they are modified astral rays and centrosome kept permanently for another function; the third, that they are entirely different from those functioning in the cell division, but have arisen in a similar way and are purely supporting fibrillæ. The appearance of the structures and their presence after such varied treatment is against the first view. It would only be possible to demonstrate which of the latter were correct if the origin of the aster had been observed. I believe they are supporting fibrillæ whatever be their mode of origin, and this is Hesse's view, he considering they are for the purpose of increasing the elasticity of the cells. This is put forward in an interesting theory of accommodation, and the fibrillæ are considered to form the antagonistic apparatus to another, to be referred to presently, which alters the shape of the lens. Between the sub-corneal connective tissue and the lens is a layer of peculiar fibres, first seen, though incorrectly described, by Patten. He made out two layers, a series of radiating fibres extending from the centre of the distal surface of the lens to the periphery, superimposed on a layer of strong circular fibres concentrically arranged (p. 581). As such do no fibres exist. Rawitz saw none here whatever, and regarded Patten's structures as artefacts ([25], p. 113). Hesse discovered the true conditions, which I can confirm with some slight additional features. There is one layer of fibres only (Pl. 7, fig. 8), and these have a kind of spiral arrangement, so that towards the centre of the lens surface they are running at almost right angles to their previous course. Near the periphery they run more or less concentrically (Pl. 7, fig. 8). They do not terminate at the centre of this surface, but continue across for some distance, and there results a series of fibres crossing one another in all directions.

In thin sections cut parallel with the plane of the cornea it is possible to see a number of nuclei here, with very deli-

cate cell-outlines enclosing them (Pl. 7, figs. 7 and 9). These cells have their ends drawn out into the long fibres seen in macerations so easily, and which are many times the length of the cell-body (Pl. 7, fig. 2). In some cases, as Hesse pointed out, a number of fine parallel fibrils appear to pass out of and through the cells (Pl. 7, fig. 7). He regards the fibres as muscle-fibres, and the cell-body as containing the remaining myosarc and nucleus. This view is based on the reaction to picric acid—säurefuchsin, which stains muscle yellow and connective-tissue red. I was not sure that they were not connective tissue cells, and in fact believed them to be such. For this reason Mallory's connective-tissue stain was used as recorded on p. 53. The fibres and cells were stained by this process an intense red, against the blue sub-corneal tissue above (Pl. 7, fig. 7). They stain therefore as muscle-fibres. Hesse says ([**34**], p. 397) that these fibres extend to the edge of the lens but not further.

The same fibres, however, are to be found in the connective tissue extending down the sides of the optic vesicle (Pl. 6, fig. 1, *M.f.*) and often quite near or even on the inner surface of the same. I believe they have a far wider distribution than Hesse supposed. This is the apparatus that, aided by the lens-cells, is (according to Hesse) concerned with accommodation. Through the contraction of these fibres the outer surface of the lens becomes reduced in extent, the lens-cells are compressed together here, and, being plastic, change their shape, the contents swelling towards the inner surface where there is less tension. The result is an alteration in the shape of the lens and hence of the focus. If the muscles are relaxed the elastic cells (aided by the fibrillæ) return to their previous shape and the focus is adapted for more distant objects. No physiological proof has yet been brought to support this theory, and, as far as experiments go, I could find no evidence of accommodation (see p. 102).

Hesse has built up his theory simply to account for the fibres on the lens and the persistent astral rays in the cells. The function of the latter may be simply to give greater

rigidity to the lens, and if the former were accommodation muscles one would expect a more definite and efficient arrangement. The same red-staining fibres can be traced, however, down the sides of the optic vesicle in the connective tissue, and those present between the lens and cornea may be simply for the purpose of tying the lens to the subcorneal layer. Before leaving the lens it will be advisable to refer to another condition seen in some of the lens-cells. This is a peculiar condition of the nucleus (perhaps pathological) observed in one or two cells in preparations fixed in von Rath's fluid and also in Hermann-sublimate mixture (preparations stained with Heidenhain's iron hæmatoxylin). The latter specimen was an eye from a small P. opercularis or P. varius. The nucleus (Pl. 7, fig. 6, *a, nuc.*) is perfectly spherical and much larger than the normal ones. The size of the normal nuclei was 5·3 μ by 4 μ (they are oval in shape), whereas the spherical ones attained a diameter of 10·6 μ. These nuclei were homogeneous, not staining deep black as the normal ones, but rather grey, slightly darker than the cytoplasm. A very delicate nuclear membrane appeared to be present with the remains of deeply stained chromatin substance attached to it. The cells containing these nuclei do not look distorted nor vacuolated by fixatives and the nucleus appears perfectly natural; no other stages could be found connecting these with the normal nuclei.

The Retina.

The retina, being the recipient region of the eye, is of great interest, and this is increased by the wonderful complexity for an invertebrate and by the numerous conflicting views that have been published as to its histological structure.

I agree with Rawitz when he said that to Patten must be given the credit of solving much of this structure. He was the first to reduce chaos to order, and though he was unfortunately carried a little too far by his imagination, he published a very creditable work, especially since very little

was known previously about this part of the eye. I believe, also, that most of Patten's good work was due to the great use of maceration preparations, though perhaps owing to the more primitive methods of section work he did not check his results as much as he possibly could by this means. It is a great pity, therefore, that his description should have been couched in terms which, accentuated by his theories, did much to bring the whole paper into some disrepute.

The retina covers almost exactly half of the interior of the optic vesicle, and since it is of considerable thickness compared with the size of the eye there is not much space left in the proximal hemisphere. The retina and underlying layers will be considered together. They are separated from that part of the eye previously considered by a membrane, the septum, first discovered by Krohn (**5**).

This septum is a homogeneous sheet of connective tissue which is slightly thicker in the middle than at the sides, and at the periphery it appears to become continuous with the inner wall of the proximal half of the optic vesicle, that part termed the "sclerotica" by Patten (Pl. 6, fig. 1, *Sc.*). This author described it as cellular, but no traces of cells or nuclei are to be seen, though the corresponding structure in the eye of Spondylus is formed of distinct cells. Patten also stated that it was double. This has not been alluded to by other observers, but I thought I had detected this double nature (**44**). I have since found out my error and I believe also the cause of Patten's mistake. He writes that the distal branch of the optic nerve, which lies across the septum, has no sheath, since the latter terminates where the nerve enters the optic vesicle. The nerve, however, has a distinct sheath, and this accompanies it to the middle of the retinal surface, where just as the nerve branches (Pl. 7, fig. 18) and spreads out over the centre, the nerve-sheath spreads out too, covering all the diverging nerve-fibres which lie therefore between two sheets of connective tissue, the nerve-sheath above and the septum below (Pl. 6, fig. 1). This nerve-sheath fuses with the septum, and I think the two sheets of tissue were

regarded by Patten as both belonging to the septum. In preparations stained by Mallory's method the blue connective tissue is brought out very distinctly against the retina, whose elements are stained red, and hence both septum and nerve-sheath can be easily followed. In some sections there appears to be a delicate concentric striation in the septum, but this is all the structure to be made out. The distal branch of the optic nerve penetrates the septum, the fibres boring through separately.

The retina has been divided into several layers by previous writers, but anatomically as well as for purposes of description it will be better to consider it as made up of two layers only:

(1) The outer layer of distal sense-cells with their interstitial supporting cells (Pl. 6, fig. 1, *D. S.*; Pl. 7, fig. 13, *O. I. c.*).

(2) The inner layer of rod-cells and their continuations the rods, together with interstitial supporting cells (Pl. 6, fig. 1; Pl. 7, fig. 13, *R. C.* and *I. I. c.*).

A table is appended (p. 77) giving the synonyms that have been used, which shows also the gradual changes that have taken place in our knowledge of these structures.

Hensen (**13**), as will be seen from the table, placed all the cells present in the retina distally to the rod-cells and rods in one category, called this stratum the "first cell layer," and said it was composed of one or two layers of spindle-formed cells, whose contours were not very distinct. The layer of rod-cells was called the "second cell layer" and the nuclei of the inner interstitial cells considered to be their nuclei.

Patten found that the outer cells of Hensen were not all of the same shape. He supposes, however, that physiologically they are alike and calls them all outer ganglionic cells. Of these he described three types, one of which had broad ends bearing many fibrous processes which penetrated the septal membrane and became continuous with the nerve-fibres of the distal branch of the optic nerve.

One of his most important discoveries was the finding of the interstitial cells of the rod-cell layer, which he termed "inner ganglionic cells" (Pl. 7, fig. 13, *I. I. c.*). Only the

Terms used in Descriptions of the Retina.

Hensen, 1865.	Carrière, 1885.	Patten, 1886.	Rawitz, 1888.	Schreiner, 1896.	Hesse, 1900.	Present paper.
Erste Zellenschicht	Schicht der spindelförmigen zellen	Outer ganglionic layer	Ganglienzellenschicht	Äussere Ganglienzellenschicht	Distale zellen	Distal sense-cells.
					Zwischenzellen	External interstitial supporting cells.
—	—	Inner ganglionic layer	Secundäre ganglienzellen	Innere ganglienzellenschicht	Zwischenzellen	Inner interstitial supporting cells.
Zweite zellenschicht	Stäbchenzellen	Retinophoræ.	Stäbchenzellen	Stäbchenzellen	Stäbchenzellen	Rod-cells.
—	Siebmembran	Terminal membrane[1]	Grenze von Stäbchen und Stäbchenzellen	Aüssere Siebmembran	Siebmembran	—
Stäbchen	Stäbchen	Rods	Stäbchen	Stäbchen	Stäbchen	Rods.
—	Substanz zwischen Stäbchen	Outer part of rods	Mantel des Stäbchens	Mantel des Stäbchens	Zwischensubstanz	Rod-matrix.
—	—	Vitreous network	—	Innere Siebmembran	Deckmembran	Basement membrane.
Tapetum	Tapetum	Argentea	Tapetum	Tapetum	Tapetum	Tapetum.
Pigment stratum	Pigmentschicht	Tapetum	Pigmenthaut	Pigmentschicht	Pigmentschicht	Pigment layer.
—	—	Sclerotica	—	—	—	Outer modified wall of optic vesicle.

[1] This supposed structure is not exactly equivalent to the "Siebmembran" (see text).

nuclei of these cells had been seen before and they were thought to lie inside the rod-cells.

Rawitz agreed with Patten in almost all respects, but made a retrograde step in asserting that a division of the outer cells into three types was unnecessary because "die gesamten Zellen dieser Schicht vollständig einander gleichen, abgesehen natürlich von den nebensächlichen Differenzen im äusseren Habitus, und weil sie, vielfach miteinander in direkter Kommunikation stehend, eine physiologische Einheit repräsentieren." Schreiner also refers to the two layers of ganglionic cells (the outer being a mixed layer, see table, and the inner one the non-nervous inner interstitial cells), and states that the outer layer is four or five cells deep in the middle of the retina. He noticed, however, that the cells of the outermost row (Patten's first type) differed from the others, though considers that all are of the same physiological nature. Hesse in 1901 (**34**) was the first to upset the prevalent ideas of these cells. He stated that there was only a single layer of cells, and that the fibres of the distal nerve were not connected with them. Hesse had forgotten, however, that the previous observers would also have considered the outer ganglionic layer to be of but one layer of cells if they had only meant it to include the cells of Patten's first type. The other cells Hesse alludes to as being pushed in between those of the outer row, which he states are of epithelial-like nature. In any case, to Hesse belongs the credit of having separated off the outer interstitial cells from those of the most distal layer, and breaking up the idea that all were ganglion-cells and alike in function.

In addition to the difference in shape and the fact that the outer cells bear cilia-like processes (Pl. 7, fig. 13, *D. S.*), he also noticed that the nuclei of the outer cells were somewhat different from those of the others, now termed "Zwischenzellen." This difference has often been very apparent to me, and it is strange that the earlier writers missed this point unless fixation and staining of these cells had been rather indifferent.

Hesse finally noticed the resemblance of these outer interstitial cells to the inner ganglionic cells of Patten, Rawitz and Schreiner, and called all of them "Zwischenzellen," stating at the same time that they did not bear exactly the appearance of nerve-cells, but his preparations showed that the fibres of the distal nerve arose from them. He did not regard them as ganglion-cells but considered them to be optic sense-cells. The function of the outer cells is not stated, but they are not supposed to be connected with the distal branch of the optic nerve.

The next mention of these cells occurs in Schneider's 'Text-book of Histology' (**38**). Schneider finds no connection existing between the "Zwischenzellen" and the distal branch of the optic nerve, nor any junction of the latter with the outer layer of cells, but finds that the nerve-fibres penetrate between them and cannot be traced further. He also describes how at the edges of the retina the cells of the outer layer at various places surround, collar-like, branches of the nerve. I believe this (see his illustrations, p. 560) must have been caused by artefacts. The interstitial cells are not considered to be sense-cells.

In 1904 appeared Hyde's remarkable account of the nerve-endings in the retina, which really caused my attention to be drawn to the Pecten eye. Hesse had previously stated that methylene-blue methods had failed him, but that the problems of the retina would in all probability be solved by the attainment of success with this stain. According to Hyde, methylene-blue methods were perfectly successful and solved all, the result being a description of the retina which stands in striking opposition to all previous work. Hyde finds that the inner interstitial cells are the nerve-cells connected with the axial fibre of the rods, and only mentions one row of outer cells which are supposed to be connected to the fibres of the optic nerve.

So much for the outer cells; I shall have occasion to make further reference to Hyde's work later. In 1908 Hesse refers again to the Pecten eye (**43**), and now finds a connection

existing between the distal cells and the distal branch of the optic nerve, so that these are also included as sense-cells, but his views of the interstitial cells remain unaltered. He had apparently neither seen nor heard of Hyde's paper, which has remained, therefore, uncriticised. Such is the mass of conflicting evidence at present existing. There is no doubt that the relation of the distal nerve to the outer distal cells and interstitial cells is the most difficult histological problem of the retina. It is extremely difficult to trace the endings of the nerve-fibres in sections, and impossible to make out the shape of the interstitial cells. I have been able to make out, however, the shape of the latter from macerations, and to trace the extent of their branches, which can be confirmed by sections. A schematic figure has been built up from macerations and sections which shows the relation of the cells to one another (Pl. 7, fig. 13).

The structures are as follows: The distal surface of the retina is bounded by a single layer of cells (Pl. 7, fig. 13, *D. S.*), the distal cells of Hesse, and the first type of Patten's outer ganglionic cells. They are somewhat regularly placed so that an epithelial-like layer is formed. The outer ends of these cells, which are directed towards the septum, are broad and bear cilia-like processes, so that a space exists between septum and cell-layer, which is crossed by the nerve-fibres from the distal nerve and filled by the processes of the distal cells, which for the most part do not reach the septum (this may be caused, however, by breakage of the fine processes during fixation). The cells are cylindrical, transverse sections cut in the plane of the retina, being perfectly circular (Pl. 7, fig. 16, *D. S.*). Their lower ends are rounded, and in some cases appear to terminate in a short pointed process. This, however, could not be followed far, and I have only seen it in some maceration preparations.

The cell contents are finely granular. Dark-staining granules (basal granules) are present at the bases of the cilia-like processes (Pl. 7, fig. 13), and these sometimes produce the appearance of a dark-staining edge. There are also

delicate longitudinal fibrillæ in the protoplasm of the distal ends of the cells, running to the bases of the processes (Pl. 7, fig. 13, *D. S.*). Like Hesse I have found no motion of the processes in living cells. Between the cells pass branches of the distal nerve, which can be traced quite easily through the septum, but with great difficulty in the retina, where it has been uncertain whether they entered into connection with the outer cells, interstitial cells, or ended free.

I think it is certain that they terminate, however, in the distal cell-layer and become connected with the cells, not by the cilia-like processes, but to their sides (Pl. 7, fig. 13). It is easy to see in sections the nerve-fibre passing to the side or apparently one corner of the distal cell, and in macerations each distal cell can be seen to possess a long, thicker process which appears to arise at the edge of the distal end, but can often be traced some distance down the side wall. This is unfortunately very difficult to make out, but is confirmed, I think, by the character of the distal cells, which are those of sense-cells, and by sections of young eyes, where the interstitial cells are only slightly or not at all developed (as noticed by Hesse).

The nucleus requires special consideration since it differs from that of the interstitial cells. Fig. 16 (Pl. 7) illustrates a transverse section through distal and interstitial cells stained with Mallory. The nucleus of the first-named (fig. 16, *D. S. n.*) is large, perfectly round, and contains a number of small chromatin granules, which stain orange red (orange G. and säurefuchsin) in addition to the distinct nucleolus which is always present and stains more distinctly orange (there may be two nucleoli present). The cytoplasm is stained red. These nuclei are very similar in appearance to those of the rod-cells to be considered below and to the nuclei of nerve-cells from the various ganglia. The character of the outer interstitial cells (fig. 13, *O. I. c.*) is very different, and I have termed them "supporting cells." They bear no resemblance to sense- or nerve-cells, and no connection between them and the inner interstitial cells or the fibres

of the distal nerve could be found. The isolated cells obtained by macerating the retina in chloral hydrate solution are illustrated in fig. 15 (Pl. 7), but these were only obtained on a few occasions and after a long search, for it is most difficult to separate them from the distal cells.

The cell-body is very small and there is but little cytoplasm left surrounding the nucleus, but from this extend long branched processes. The nucleus retains the blue stain after Mallory when it has been taken from the nuclei of the distal sense-cells, and generally it may be said that the interstitial cell-nuclei stain darker and are more homogeneous, it being more difficult to resolve the granules. They are furthermore flattened and are only about half the size of the sense-cell nuclei. The processes lie in close contact with the distal sense-cells, there being often two clasping them and extending between them towards the septum (Pl. 7, fig. 15, *a*.).

From the proximal end of the cell may arise one or more irregular processes which branch and penetrate some distance between the rod-cells. It is quite easy to understand how these long processes, which in my opinion tie and support the sense-cells, have been for a long time considered as nerve-endings, either of nerve-cells or of the fibres from the distal nerve. In many ways the interstitial cells resemble in shape and staining the neuroglia cells found clasping the nerve-cells in the various ganglia of Pecten and other lamellibranchs. The outer ganglionic layer of Patten is composed, therefore, of two types of cells—sensory cells forming an outer layer and connected with the distal nerve, and supporting non-sensory cells interpolated between them. Miss Hyde did not recognise the latter at all. I have had no success with methylene-blue methods, but I do not think they would be of much advantage unless fixation was very good (a thing not by any means easy to attain with many special methods), for it would be almost impossible to check the results and to determine whether, in the confusing mass of fibres, nervous or both these and non-nervous processes had taken the stain.

We have now to consider the second sensory part of this

remarkable retina, innervated by the proximal branch of the optic nerve. This region is most obvious in sections and is composed of a row of pillar-like rod-cells, bearing rods, with a series of interstitial cells lying between the former and once supposed to be their nuclei.

The rod-cells (retinophoræ of Patten) (Pl. 7, fig. 13, *R. C.*) occupy a very large part of the retina. In very young eyes, however, the distal cells are more prominent and occupy a proportionately much larger part. They are extremely long cells, especially those situated in the centre of the retina. The outer ends, to be found at the periphery of the retina, are attenuated and pass gradually into the nerve-fibres of the proximal branch of the optic nerve (Pl. 6, fig. 1, *Op. P.''*), so that it is impossible to say where one ends and the other begins. From this point they increase in thickness, the first third of their length or more lying almost horizontally under the outer layers of cells, embraced by the processes of the supporting cells. Some little distance from the periphery, not very different for cells from different parts of the retina, each swells rather suddenly round its nucleus (Pl. 7, fig. 13, *R. C.n.*), and from this point the thickness remains practically the same to the basal end, though there is a slightly more constricted part below the nucleus. All the rod-cell nuclei are situated in a scattered cluster not far from the edge of the retina, so that the nucleus is nearer the proximal end in rod-cells belonging to the centre of the retina, whilst in the middle or slightly nearer the base of rod-cells from the peripheral regions.

The distal cylindrical portions of the rod-cells lie parallel with one another, perpendicular to the plane of the retina, and terminate at the same level, forming a well-defined line between them and the layer of rods. This line (Pl. 7, fig. 13, *S.m.*) has been described as the section of a membrane (see table), which extended across the retina and was pierced by the rods (Pl. 7, fig. 13, *Rod*). These are direct continuations of the rod-cells, and rod and rod-cell form together one entity—the product of one cell. Patten described a delicate

membrane supposed to separate the protoplasm of these two parts, but there is no trace of one, and the cell contents of both are continuous.

The appearance of two definite structures separated by a membrane is due to an external flange or projection existing on the wall of the rod-cells at their junction with the rods, by means of which adjoining rod-cells are connected. This produces in sections the effect of a "sieve-membrane" with circular holes through which the rod-cells and rods protrude.

It is a rather difficult point to decide. Hensen, so far back as 1865, said that by reason of the rod-cells ending at the same level a sharp bounding line was formed, which could easily be mistaken for a membrane, but this was not present. Patten did not see it either, but, as stated above, believed there was a delicate membrane, the "terminal membrane," in each rod-cell. Rawitz found no membrane either inside or external to the cells, but Schreiner and Carrière both affirmed its presence. Hesse (**34**) refers to a sieve-membrane, and on p. 409 he remarks that in some specimens of P. jacobæus and P. maximus the inner interstitial cells can be followed up to the sieve-membrane, which is possibly a product of these cells.

In my opinion the sieve-membrane is, as above stated, due to the extended walls of the rod-cells, and has no part from the interstitial cells. This line is usually well marked in the marginal regions of the retina, where there are no rods borne by the rod-cells (Pl. 6, fig. 1, *M. ret.*). Where necessary, the well-marked line above referred to will be called a "pseudo-sieve-membrane" for convenience in description. In macerations of the retina, in $\frac{1}{50}$ per cent. chromic acid (the preparations being stained with picro-carmine and examined with the oil-immersion) a series of very delicate parallel fibres could be seen running longitudinally on the surface of the rod-cells (Pl. 7, fig. 13, *Cells A*). It was not possible to follow them proximally to the nucleus. At the junction of rod-cell and rod they bear thickenings (Pl. 7, fig. 13, *S. m.*),

which stain more distinctly, and it is probably these only which form the "flange" and the attachment of rod-cells to each other.

The fibres are supporting fibrillæ, and in preparations where the rods had broken off (Pl. 7, fig. 13*a*) the tube of fibrils could be distinctly seen. Where the rods remained attached to the rod-cells the fibres were continued below the thickenings, but had left the surface of the rod, enclosing the latter in a kind of sheath (Pl. 7, fig. 13).

Whether they lie on the rod-wall in the normal condition or in the interstitial substance to be presently considered I cannot say. Another point concerning the shape of the rod-cells remains to be referred to. Above the nucleus the rod-cell does not become gradually less in diameter, but after a constriction there often occurs one or more irregular swellings, which give the attenuated end of the rod-cell a more or less varicose appearance.

Patten saw one of these and described it as a delicate oblong vesicle containing a second faintly staining and often invisible nucleus. Rawitz would not consider the presence of a nucleus, but saw the enlargement and said it might be artificial. Schreiner also figures it. It is most easily seen in isolated rod-cells, in a maceration. I find that there may be one or more, and that they are simply due to the rod-cell being flattened in places by the pressure of adjacent cells; the flattened part appears as an enlargement if not seen in edge view.

The rods are cone-shaped with the apices rounded. The base has the same diameter as the rod-cell, that is, where they are continuous, and from here the diameter gradually decreases towards the lower end, though at first very gradually. They are separated and surrounded by a homogeneous substance (Pl. 7, fig. 13, *R. mat.*), which fills up all the cavities that would otherwise have remained between them, and also forms a layer below them. This substance is stained black by iron hæmatoxylin, it is blackened by osmic acid, and is stained blue by Mallory's connective-tissue stain. I believe

it is a semi-fluid substance of connective-tissue-like nature, which contains some oil or fatty body, and I have called it the rod-matrix (Pl. 7, fig. 17, *R. mat.*).

Patten described the rods, which are very difficult to preserve, as consisting of a "hyaline refractive sheath surrounding a pyramidal axial core filled with a watery non-refractive fluid, and a short distance from the inner ends of the rods, terminating in a rounded apex" ([**22**], p. 585). This axial core is, in my opinion, the true rod, and what he described as the sheath is the surrounding rod-matrix. Carrière (**21**), had noticed this before Patten, and described the rods as being immersed in a fatty substance. Patten, however, adds that this was due to the fusion of the sheaths of the poorly preserved rods. Rawitz agreed with Patten about this sheath, though he differed slightly in regard to its optical properties, and Schreiner also does not accept Carrière's view. Hesse's view is, however, the same as mine, and he has emphasised the error of Patten, Rawitz, and Schreiner, whose peculiar idea of the rod was due to the fact that they believed an outer sheath to be necessary. The rod structure differs from that of the rod-cell in the fact that there is much less stainable protoplasm, and this is usually aggregated round an axial fibre (Pl. 7, fig. 13, *Ax.f.*). It will be unnecessary here to go into further comparisons of the previous views on these structures. The rod-cells have been described almost correctly, though with deficiencies by most observers, with the great exception of Hyde, whose account I am leaving until later.

In sections of well-preserved rod-cells and rods, such as those fixed in Bouin or Zenker and stained in Mallory's stain, an axial fibril will be easily seen running through the rod. It is with reference to this structure that most of the confusion has arisen. Patten stated that each rod-cell contained an axial nerve-fibre which entered the attenuated end, passed through the first vesicle-like swelling, passed the large nucleus, and went on down to the lower end of the rod, whence it issued, and divided into two main branches which

became connected with the axial fibres of neighbouring cells (see Patten's fig. 140, Taf. 32). Furthermore, he describes how towards the lower ends of the rod-cells the axial nerve-fibre begins to give off radiating fibrillæ, which are so numerous in the rods as to constitute the greater part of their substance. Hensen was the first to see the axial fibre in the rod. Patten figured it as being equally distinct and of the same diameter in rod-cell and rod. Rawitz found, however, that there was a fine canal running through the former in which lay the fibre, which, he adds, is the continuation of a nerve-fibre from the proximal branch of the optic nerve. This central canal and fibre was supposed to be present in the rod but terminated without the complicated connections of Patten. Carrière, in his second paper (an answer to Patten's criticisms of his first) (**26**), could not bring the existence of a nerve-fibre inside a cell into line with histological teaching, and hence said that what was present was simply a differentiation of the cell-substance. Schreiner came to the conclusion that a detailed examination was necessary owing to the diverging opinions of previous authors, and found after making sections and teased preparations that there was no axial fibre at all in the rod-cells, and what had been seen there was only one of the contours of a rod-cell produced by pressure causing these normally cylindrical cells to be angular. He found it very distinctly stained, however, in the rods, and it ran straight to the end where it terminated in a point. He adds that it differs somewhat in staining qualities from nervous tissue and is too thick for a nerve fibre (p. 72).

Hesse found after all this research that it was necessary to go back to the earlier views, for he made out the axial fibril running through both rod-cell and rod.

He states, however, that it is far more easily seen in the rods, and even there it varies in the same preparation.

It is less distinct in the rod-cells because thinner (except in P. aratus), and in some cases Hesse saw more than one present. This bring us to Hyde's views (**39**) regarding rod-

cell, rod, and axial fibre, which are based on methylene-blue methods. It appears somewhat difficult for me to understand how the material presumably stained could remain in good condition for four years until taken up for completion.

We are told that a rod consists of a nerve-cell whose small anterior end (upper end ?) projects slightly beyond the median limiting membrane, and whose much elongated posterior portion is tubular and bluntly terminated. This portion is encased in a hyaline sheath, with the end capped by a homogeneous cuticular substance, which in methylene-blue preparations appears like the matrix separating the rods. A small nucleus lies in the anterior end of the rods and from this an axial fibre extends to the posterior (lower end).

There is another series of important elements in the retina —"bipolar cells." These extend from the median limiting membrane (presumably the same as the line dividing rod-cells from rods) outwards towards the margin of the retina. "Their large granular elliptical nuclei may be seen in longitudinal sections extending in a row, a short distance from the median limiting membrane. The whole cell with its afferent and efferent axon is encased in a hyaline sheath, under which are scattered blue granules of various sizes." The rest of Hyde's conclusions are difficult to understand, but putting figures and descriptions together, one gathers that the rod-cells of all previous writers are the same as certain "supporting cells of the median layer" of Hyde. The bipolar nerve-cells above referred to are the inner interstitial cells (Pl. 7, fig. 13, *I. I. c.*) or inner ganglionic cells of other authors, and from them arise two fibres, one of which runs to the edge of the retina and the other to the pseudo "sieve-membrane," following the course of the median supporting cells of Hyde and lying between them. These are the afferent and efferent axons. Distally the afferent axon has a dendritic termination, which comes into relation with the upper end of the axial fibre of the rod. Proximally the efferent axon terminates with other efferent axons in a common large ganglionic cell. These marginal ganglionic

cells, besides connecting up various axons of bipolar cells, give off fibres which make up the proximal branch of the optic nerve. This means in short that the sensory structures (the rod-cells) of all other writers are merely median supporting cells, the inner ganglionic cells of Patten and Rawitz (the interstitial supporting cells) are bipolar nerve-cells, and the marginal ganglionic cells of Hyde have not been seen by any other investigators. Patten and others must have mistaken, adds Hyde, the axons of the bipolar cells for axial fibres in the rod-cells!

I took some little trouble to see if it were possible for any of these results to be correct, though from à priori reasons, assuming a little of the previous work to be satisfactory, it appeared very doubtful.

In the first place Patten and his successors could not have seen the bipolar cell axon inside a rod-cell, since they all described it as being outside and possible of separation in teased preparations.

In the second place, the bipolar cell of Hyde has always been described as multipolar, and hence though two long afferent and efferent axons might have been missed, her predecessors had a better idea of its true shape. Finally, since rod-cell and rod are in direct continuation it is impossible for the axial fibre of the latter to become connected with the process of a cell lying between the former. The results are, in fact, impossible. The rod-cell in its general features I have found to be exactly as described by most other writers. The "bipolar cell" is the interstitial supporting cell to be subsequently described, and the rod contains no nucleus at all. The marginal ganglionic cells as described by Hyde do not exist. I must now refer to the axial fibre and the internal structure of the rods. The first idea striking an observer is that the true condition of things is like that described by Schreiner, viz. an axial fibre is present in the rods, but not in the rod-cells. After staining with iron hæmatoxylin, but especially after using Mallory's stain, with Bouin's fluid as fixative, traces of a much thinner fibre or fibres are to be seen

in the rod-cells (Pl. 7, fig. 13, *cells B.*). In a memoir on Pecten (**44**) I made the statement that this was probably the true condition, and I find that Schreiner in his text-book on histology (**38**) has done the same. The latter author refers to the axial fibre as a neurofibril, a structure which has risen in importance since Apathy's work in 1897 and about which very much has been written, chiefly on the continent, in the last few years. I believed that the thick neurofibril easily seen in the rods divided into numerous delicate, more elementary fibrillæ in the rod-cells, a view rendered more probable by the fact that whilst the contents of the latter are uniformly distributed, filling the cell, the protoplasm of the rods is usually aggregated in the middle. I could not at that time, however, find proof of this in Pecten, although Hesse stated that sometimes he had seen more than one fibre present.

Usually the axial fibre is thickest and stains most darkly in the upper half of the rod, though sometimes the whole length in the rod is much the same in appearance.

It begins to disappear a little below the line of junction with the rod-cells, but again sometimes extends quite as distinctly a little above this. This disappearance, or partial disappearance, is due to the separation into delicate branches which extend right through the rod-cell (Pl. 7, fig. 13, *B.*, *R.C.*).

The separation is irregular, and sometimes one fibril is left much thicker and may be followed easily through the rod-cell: presumably this feature gave rise to Patten's view.

The point of separation of the axial fibril of the rods into finer fibrillæ varies even in the same section, and in rod-cells situated near the margin of the retina (young rod-cells) the axial fibre may often be seen as thick and distinct as in the rods. In macerations in chloral hydrate solution or chromic acid and also in teased fresh material the axial fibril is seen as distinctly as in stained sections.

It is rather thick and quite stiff like a bristle in these preparations, never having normally the snaky course

ascribed to it by Hesse. Often the more delicate rod is broken up in maceration and the axial fibre is then left sticking out from the protoplasmic remains of the cell (Pl. 7, fig. 14, *Ax. f.*).

After seeing these preparations one is rather inclined to believe that this is also a supporting structure.

In sections, however, the appearances are more favourable to the nervous view. The separation of the components of the axial fibre is similar to that often taking place in neurofibrillæ, and the fibre occurs in a sense-cell and stains always like the nerve-fibres in the same preparation. In the rods the axial fibre differs somewhat in appearance from a typical neurofibril in thickness and distinctness. These structures considered as the conducting elements of the nervous system were unknown to the earlier writers on the Pecten eye.

There are two views, then, that may be taken of the function of these fibrillæ. We may regard the axial fibril in the rod as a true neurofibril, a "primitive fibril" formed by the apposition of several elementary fibrillæ which pass through the rod-cell, the apposition occurring normally or through fixation. These neurofibrillæ have, then, the function assigned to them by Apathy and Bethe—the conduction of nerve impulses. On the other hand we may consider the whole to have only the function of a system of supporting fibres. The latter view would resemble that put forward by Nansen and accepted by several investigators, who consider the neurofibrillæ to be the supporting, and not the conducting elements of the nerve-cells. It is also conceivable, of course, that the structures are not homologous with the neurofibrillæ of nerve-cells at all. There is at present, to my mind, much confusion existing in reference to fibrous structures in nerve-cells, especially since Holmgren has shown (**37**) that processes of the neuroglia actually penetrate into ganglion cells and act as supporting fibres.

An axial fibril of the same type as that occurring in the Pecten eye is a feature of the rod-cells of many other invertebrate eyes. For example, in the Lamellibranchiata it is

present in Arca, Lima, Spondylus (**34**), and Cardium (**42**); in the Cephalopoda it is probably of general occurrence. It is very definite in the rods of the Alciopiden, and has been found in the Polychaetes Nereis and Lysidice by Hesse (**33**). In Gastropods a definite bundle of neurofibrillæ has been found in the visual cells of Limax (Smith [**40**]). In other forms there occur, instead of one thick axial fibril, a number of fibrillæ which terminate in a comb-like margin ("Stiftchensaum" of Hesse). This is a feature of the distal cells of the Pecten eye, and according to Hesse is practically universal, the fibrillæ occurring also in the rods and cones of vertebrates.

The rods or analogous structures are also of widespread occurrence in optic sense-organs, though it would be difficult to homologise many of the rod-like structures with one another. Hensen, and later Grenacher, looked upon all the rods as cuticular structures, but I doubt now if any rod can be shown to be cuticular, not even the rhabdome of the Arthropods, a differentiated part of the reticular cells. Hesse regards the neurofibrillæ then as the universal actual recipient elements of the visual cell and the plasmatic part of the rod as a support for the fibrils. Experimentally it is impossible to determine whether the neurofibrillæ are the recipient elements or not, but from the constancy of their presence I believe they play a great part in this process. I have shown how in macerations the rod-cell may break up, leaving the axial fibre (Pl. 7, fig. 14). It does not appear from this as if the rod could give much support to the latter, but the true state of things in the living eye may possibly be different. I am rather inclined to believe, however, that the plasmatic portion of the rod acts conjointly as a recipient organ, and that the stimulus is passed on to the neurofibrillæ which conduct the nerve impulse wider.

I consider Hesse's estimation of the number of rods in a retina to be rather low for the large eyes of P. jacobæus or P. maximus. In the latter species there were about ten thousand in the retina of one specimen examined, and the number of rod-cells therefore exceeded this number, since the marginal ones do not bear rods.

Below the rod-matrix which underlies the rods is a limiting membrane, the basement membrane (Pl. 7, fig. 13, *B. m.*), which extends completely across the eye. It corresponds to Schreiner's "Innere Siebmembran," but is a perfectly continuous thin sheet. It is stained by hæmatoxylin similarly to the matrix but darker, and since the rods terminate a little distance above it it is obvious that they cannot pass through it. It occupies a similar position to Patten's "vitreous network," but his description also refers to a thin layer of hyaline substance perforated by large holes into which the inner ends of the rods fit, and Schreiner states that the points of the rods come to lie against the tapetum. No traces of any cell-structure have been made out in this bounding membrane, which, as noted above, is not perforated by the rods.

Reference has already been made to the marginal area of the retina (Pl. 6, fig. 1, *M. Ret.*). This is best studied from specimens fixed in Carnoy's fluid. The rods remain practically similar in size until about the tenth from the margin of the rod-bearing region, and then follows a rapid decrease in size, leading to the apparently fibrous lateral parts where no rods are present. Careful examination will reveal the fact that the so-called outer sieve-membrane can be traced to the very edge of the retina, but the space between it and the basement-membrane is exceedingly small. This corresponds, however, to the space occupied by the rods in the middle part of the retina. The axial fibre or neurofibril can be seen more distinctly in these marginal rod-cells, which for a little distance are similar in diameter to the much longer ones in the centre of the retina. They next become much less in diameter until finally the boundaries become difficult to detect, and the axial fibril is the most distinct part of the cell. It can also be seen extending below the line of the pseudo sieve-membrane, though without any rod. Between these modified rod-cells are more supporting cells.

The marginal region differs, therefore, from the central part of the retina in being composed of rod-cells which are far shorter than those of the latter region, whose diameter is

reduced, and which bear practically no rods, though the axial fibril, which is very distinct, appears to extend a little way below the pseudo sieve-membrane. I believe that this region is occupied by young rod-cells and rods, and it can be seen how the rod is a gradual product of the rod-cells, as the appearance of the former in other parts of the retina naturally suggests. The gradual increase in size of the rods at the junction of the marginal and the central rod-bearing region is well marked. Probably the former region does not play any active part in vision at all.

Hensen called this area the "Retinawülste," because of the folded appearance in sections, and Hickson's figures also show the retina in this form. I have found the same condition after several fixatives, including Von Rath's fluid and Bethe's fixative for methylene blue. It is due to contraction, and is not normal.

The inner interstitial supporting cells (Pl. 7, fig. 13, *I. I. c.*) have already been referred to several times. They lie in close contact with the rod-cells, between which they send their processes, and they are situated not far from the pseudo-membrane (Pl. 7, fig. 13, *S. m.*). Patten was the first to recognise that the nuclei of these cells really belonged to cells lying between the rod-cells; they had been considered the nuclei of the latter by his predecessors. He figured them correctly as multipolar cells, but fell into error in regard to the nucleus, just as he and most of his successors considered that all the cells between the rod-cell layer and the septum had the same type of nucleus and were physiologically alike. It is quite easy to see in preparations stained with Mallory or iron hæmatoxylin that these nuclei resemble exactly those of the outer interstitial cells. There is a considerable difference between them and the large nuclei with distinct nucleolus and chromatin granules, which are present in both the distal sense-cells and the rod-cells (Pl. 7, figs. 13 and 16, *R. C. n.* and *D. S. n.*).

The shape of the cells can be best seen in isolated retinas after macerating in $\frac{1}{50}$ per cent. chromic acid for several days

and staining in picro-carmine. There is very little protoplasm round the nucleus, and the processes are so irregular that beyond the fact that the cells are multipolar no definite shape can be ascribed to them. They are, on the whole, slightly larger than most of the outer interstitial cells. The processes wrap round the rod-cells, and may even extend through the basal pseudo-membrane between the rods. It has been said by Hesse that the inner interstitial cells are so rare in the centre of the retina that there is only one to four or five rod-cells. They are just as numerous here as elsewhere, except, perhaps, the peripheral modified region.

Patten and Rawitz considered these cells to be ganglion-cells. Schreiner figured their shape incorrectly (as did I myself in a previous memoir) and found them to be connected with the distal nerve. Hesse also believed these cells to be nervous, for he states that the connection with the distal nerve is sometimes very distinct. In his last paper, however, he has altered his views of the relations between the distal cells and the nerve, and the question of the interstitial cells is therefore left open. Hyde, as already noted, regarded them as bi-polar nerve-cells connected with the axial fibre of the rods. Everything, however, points to the conclusion that the inner interstitial cells, like the outer, are simply supporting cells, their structure being quite unlike that of nerve- or sense-cells, and no connection with nerves having been found.

Sub-retinal Layers.

Below the retina there is generally a space, a split between it and the next layer, which may be of considerable size. All writers have figured this, but it is impossible, in most cases, to discover whether they regarded it as normal or not, since only Hesse refers to it, and he regarded it as due to shrinkage. I have figured it as it usually occurs in sections (Pl. 6, fig. 1), but it must be remembered that this space is simply due to fixation, etc. In some cases, for example, the next layer, the tapetum (Pl. 7, fig. 1, *Ta.*), will be found for some distance

attached to the retina, and then will occur a stretch where it has evidently been torn off, and remains attached to the underlying pigment-layer (Pl. 6, fig. 1, *Pg.*). This layer is also very often pulled away from the wall of the optic vesicle, and, whilst remaining attached to the tapetum, leaves fragments adhering to the wall, indicating where it once has been. In the normal eye, retina, tapetum, and pigment-layer are all in contact with one another, and no space occurs between the latter and the wall of the eye.

The tapetum.—This layer is very conspicuous both in the living eye and in sections, and was very early discovered by Krohn (**5**). Hensen stated that it consisted of polyhedral cells. Patten called it "the argentea" (a name which I previously employed, but since "tapetum" is more correct by order of priority I have gone back to it). It is unfortunate that the term "tapetum" has been used to designate two different layers.

Hickson and Carrière believed the structure was formed of a number of fine fibres crossing at right angles. Patten considered it to be a modification of two layers of cells into refractive laminated membranes composed of minute square plates. Hesse found the tapetum to contain always a single nucleus surrounded by some residual protoplasm and therefore derives this layer from a single large cell.

The tapetum is made up of several layers of minute square plates (Pl. 7, fig. 19), which are yellow by transmitted light and reflect the light like silvery plates.

This gives the diamond-like lustre to the living eye, and I have even a series of transverse sections, mounted in canada-balsam, which retain the same property. The layer is thickest in the centre and shades off gradually to a very thin peripheral region, which can be traced between the retina and the pigment-layer to the wall of the optic vesicle.

I have been unable to trace Hesse's nucleus, and in adult eyes it is impossible to detect any remains of cells. I believe rather that this layer is formed by the underlying pigment containing cells or by other cells which disappear, but more

probably by the former, since some of the granules contained in these cells may resemble the substance of the tapetum.

The pigment layer was also an early discovery because of its conspicuous appearance, and it is often possible to see the red pigment through the substance of the eye-stalk if there is little pigment in the epithelium of the latter. This layer was Patten's tapetum. Hickson had regarded it as a fluid with no cellular elements at all. Carrière thought it was a continuation of the septum, and Rawitz describes it as being differently coloured in the various species. Schreiner explains Hickson's view on the grounds that in P. maximus, which he examined, the pigment was really a fluid mass containing large and small granules, but adds that in other species this layer is a single or double row of rather large polygonal cells.

I have investigated several species and find that this layer is cellular in all, though the boundaries of the cells may be difficult to see in the adult. In young specimens of Pecten, only a few millimetres in diameter, the pigment-layer appears to be composed of a single layer of epithelial-like cells with little or no pigment present.

As the eye grows the pigment increases, the cells become filled and usually very irregular in shape, so that in large eyes of P. maximus the epithelial arrangement persists often only in the marginal part, and in the middle the layer may be irregularly two cells thick.

The actual colour of the pigment is of little importance, since it varies in specimens of the same species and often in cells of the same eye. It is some shade of red-brown, and generally the cells are filled with a finely granular dark brown pigment, but with here and there frequently large, more darkly coloured bodies, like round concretions (Pl. 6, fig. 1, *Ta. c.*). There are large and small bodies of this nature, and sometimes also iridescent granules resembling in appearance the substance of the tapetum. The nuclei are best seen in iron hæmatoxylin preparations. In P. maximus

they are round and contain a conspicuous nucleolus together with scattered chromatin granules.

The cells of the pigment-layer appear to be continuous with the retinal cells at the periphery of the retina. Patten considered this layer, in fact, to be homologous with his outer ganglionic layer. I am unable to say whether it should be considered as a modified continuation of the distal sense-cells or of the outer interstitial cells. The nuclei are much more like those of the former, but the development of the Pecten eye still requires elucidation. This completes the account of the structures enclosed in the optic vesicle. A reference must be made here to the inner wall of the proximal hemisphere of the latter. It is formed of connective tissue, and Patten called the surface layer the "sclerotica" (Pl. 6, fig. 1, *Sc.*). He described it as a two-layered, tough, hyaline, connective-tissue membrane continuous with the septum.

Rawitz disagreed entirely with this and objected to the term "sclerotica," because of its inappropriateness, considering the use of this term in the nomenclature of the vertebrate eye. This membrane of Patten is, however, well marked in longitudinal sections of the eye, though it is simply the limiting or surface layer of the connective tissue of the eye-stalk and directly continuous with it. In sections stained with Mallory's fluid it is very conspicuous (Pl. 6, fig. 1, *Sc.*), and stains a deep blue against the light blue of the ground tissue of the eye-stalk. It also differs from the latter in being hyaline and containing neither fibrous elements nor nuclei. The connective tissue forming the wall of the distal part of the optic vesicle lacks this differentiated surface layer entirely. In reactions to several stains it resembles the septum, and it also appears to be continuous with this membrane. The layer is thus obvious, but is not to be considered as a separate structure in Patten's sense, and the term "sclerotica" is certainly inapplicable.

I have called it simply "the modified connective tissue-wall of the optic vesicle." It must be remembered that the terms "cornea," "sclerotica," "iris," etc., used by Patten and others

cannot be compared directly with those designations in the vertebrate eye, for the structures bearing these names are not homologous, and in fact the whole structure of the eye is not to be homologised with that of the vertebrate optic organ. The resemblances are pure cases of homoplasy, and there is absolutely no proof of a genetic community of origin.

Innervation and General Conclusions.

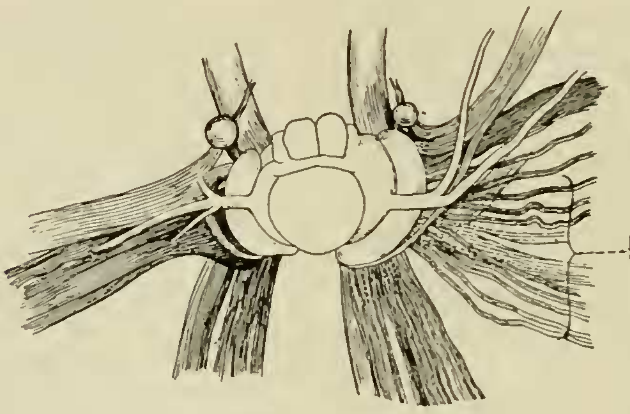
It has already been pointed out that the retina is innervated by two branches of an optic nerve which passes down the centre of the eye-stalk (Pl. 6, fig. 1; Pl. 7, fig. 2, *Op. N.*).

This nerve has been considered as an offshoot from the circumpallial nerve. In sections which cut the optic nerve obliquely, so that only a small part appears in a section, this may very easily appear to be the case, but if a section cuts the mantle exactly in the plane of the optic nerve, so that a long stretch appears in one section, it will be seen that the real state of things is somewhat different. At irregular intervals nerves pass radially through the mantle-lobes (between the radial pallial muscles) from the visceral ganglion to the circumpallial nerve (Pl. 7, fig. 2, *Circ. N.*). Some of the fibres of these nerves pass into the latter, but at certain places (below the eye-stalks) the bulk of the fibres pass round the circumpallial nerve (on the shell side of it, Pl. 7, fig. 2), touching it, but not entering it, and these innervate the eye. Some fibres appear also to leave the circumpallial nerve and to enter this optic nerve, but it will be evident that most of the nerve-fibres come directly from the visceral ganglion.

Now the visceral ganglion of Pecten is extremely complicated in build and I think unique among the Lamellibranchiata. No details will be given here, since a paper is being prepared on this subject, but it will be seen from the figure (text-fig. 1) that there are several lobes, of which two lateral ones are very conspicuous. From these radiate out on either side the pallial nerves (*Pall. N.*). The ganglion is asymmetrical, the left lateral lobe being larger than the right, and

it is from these lobes that the nerves arise which innervate the eyes. It is interesting, therefore, to observe how the development of the eyes has affected the ganglion, for in P. jacobæus and P. maximus, where the number of eyes on the left mantle-lobe exceeds that on the right, the left lateral lobe of the visceral ganglion is considerably larger than the right, especially in the former species, whereas in P. opercularis, where the number of eyes is more equal on both sides, the left lobe is but slightly larger than the right. Probably the presence of both lateral lobes is due in the first instance to the great development of pallial structures.

TEXT-FIG. 1.



1.

The retina of Pecten is of the inverted type, that is (like the vertebrate eye), the recipient bodies, the rods, are directed towards the tapetum, and away from the source of light (text-fig. 2). In addition to this feature we have a complexity only paralleled in a few cases in the invertebrata (and even then without the inversion), for there are two series of recipient cells. Inversion occurs in the Platyhelmia, though the eyes are much simpler than the Pecten eye. In the Lamellibranchiata the eyes are either absent or much more simple as a rule than the eye of Pecten, but we have as a matter of fact the two eyes most like the one we are considering in this group, namely, the pallial eyes of Spondylus, which are practically the same as Pecten, and the eyes

(siphonal) of Cardium. In both cases there are two series of recipient cells and the retinas are inverted.

There are some interesting analogies; thus, for example, the ocelli of Agrion (a dragon fly) possess a retina which has also two series of recipient cells very like the rod-cells with rods and the distal cells of Pecten, but there is no inversion.

Text-fig. 2.

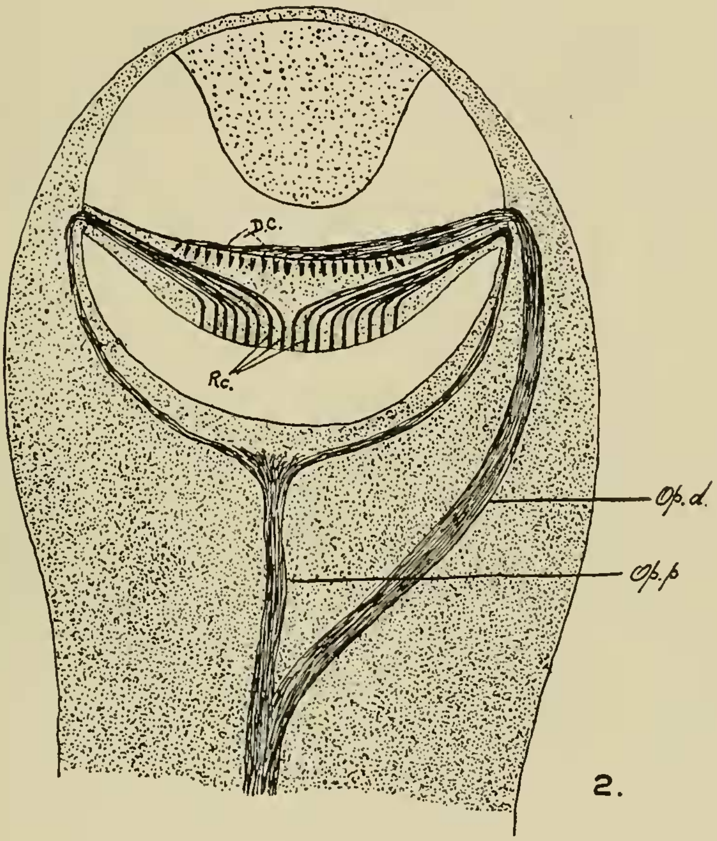


Diagram showing distribution of Nerve elements in Eye
Op.p. Optic Nerve, proximal branch. Op.d. Distal branch of Optic Nerve
D.C. Distal Sense Cells. Rc. Rod cells with Rods.

We are also familiar in the vertebrate eye with two kinds of recipient structures—the rods and cones—though these bodies are situated in practically the same layer (Bernard [36] has, however, stated that in Amphibia the cones are earlier stages in the development of new rods).

When all things are taken into consideration the eye of Pecten and also of Spondylus appears a very remarkable

development, especially for a Lamellibranch, and the complexity of structure, together with the large number of eyes, has been a difficulty felt by most writers who have sought for an explanation of these organs. Patten put forward an extraordinary theory, calling the eyes "heliophags." It is hardly necessary to go into this here, since a criticism appeared in the 'Quarterly Journal of Microscopical Science,' vol. 27, which may be referred to.

The eyes have shown no evidence of being phosphorescent organs, though I have observed and stimulated them at night and in the dark. A shadow thrown on to the eyes of an open Pecten causes a closure of the valves, and this reaction usually takes place very rapidly, though very often the perception of light stimuli does not appear to be any better than by Arca with very simple eyes or others with pigment spots. If, however, the shadow thrown on to a Pecten does not extend over a number of eyes there appears to be no reaction, and, just as Rawitz observed some time ago, a small object quite near produces no effect unless its shadow falls on a large number of eyes in quick succession. No evidence of accommodation could be obtained experimentally. Furthermore, it is hardly possible to correlate the presence of these structures with the active habits of the animal, e.g. swimming, for Lima swims just as well as Pecten, but has extremely simple eyes. Again, Spondylus has eyes practically identical with those of Pecten, but does not swim, and the same thing applies to the only other Lamellibranch with an eye approaching that of Pecten in structure, namely Cardium. In the latter case the eyes are confined to the tentacles of the siphons. It would be interesting to determine by biometric methods whether these organs were still being kept up, or were degenerating, especially in forms like P. jacobæus and P. maximus, where there exist very small eyes side by side with the large ones.

These may be growing, or they may be eyes which have retained their young form, have not grown, and will not grow. They agree with young eyes in structure. The

variation, however, in specimens of the same size renders the examination of a large number a necessity, and I have been unable to obtain a fraction of that number. It is possible that P. jacobæus and P. maximus are more highly developed forms than P. opercularis and P. varius, for they possess no byssus, though the gland is present and they have passed through a byssus stage, and the retractor muscles of the foot, of which one is left in P. opercularis, are even more vestigial in P. maximus. If these two forms are considered older we find that there has been a reduction in the number of the eyes, for they are more numerous in P. opercularis, P. tigrinus, and other smaller forms, and this reduction has then taken place to a greater extent on the under convex valve than on the upper flat one. The increase in convexity and difference between the two valves, reaching a maximum in P. jacobæus, has been accompanied by a reduction of the eyes on the convex mantle-lobe both in number and size. These are, however, only hypotheses. The large number of eyes present is probably to be accounted for by the reason put forward by Rawitz, namely, that the actual recipient area in each eye is small, that oblique rays are cut off, and that in life the eye-stalks remain still; a large field of view is therefore only possible with numerous eyes.

The presence of two series of recipient elements has not been explained by previous writers and has in fact been usually passed over. No experiments have enabled me to state anything definitely about this, except that, as already mentioned, there appears little evidence of accommodation. It might be advisable to point out here that the removal of an animal like Pecten from the dim regions at the bottom to the daylight and shallow water of the aquarium has possibly an injurious effect, and probably it would be a delicate complicated structure like the eye that would suffer most. Hence it may be that our aquarium experiments are almost useless in this respect.

The presence of the distal layer of sense-cells as well as

that of the rod-cells and rods may be a device for increasing the area of the recipient elements without increasing to any extent the size of the retina, but more probable is perhaps the following view. There has not yet been definitely proved to exist any special apparatus for accommodation in the eye (though Hesse's theory has not been disproved). Now it may be that the two layers of recipient cells are for the reception of images of objects situated at different distances from the eye, which are focussed at different distances from the lens. Thus the image of near objects would be focussed on the rods and that of distant objects on the outer distal cells. A similar condition would apply to the ocelli of Agrion, and, in fact, Hesse describes such (**35**), but adds, "Ich kenne nirgends eine ähnliche Einrichtung." In the Heteropod eye there also appears to be a device for the reception of rays from objects at different distances from the eye. There is, however, only one series of cells, but the free ends bearing the comb-like margins are turned so that they are at right angles to the plane of the retina, and some are nearer the lens than others.

The development of the Pecten eye still remains incompletely known, and Patten's observations need confirmation. The derivation of the various layers will certainly throw much light on the structure of the adult eye and the inversion of the retina. Unfortunately the material for such a research is somewhat difficult to acquire as all the elements are formed in extremely young specimens, and I have been unable therefore, so far, to follow out this line of inquiry.

It will be perhaps useful if the most interesting features in the general structure of the Pecten eye are summarised here and a few comparisons made with other eyes, which may bear some resemblance to the former. The eye is a closed vesicle; there is a cellular cornea continuous with the surface epithelium, and below this a cellular lens. The retina is made up of two series of recipient cells innervated by two branches of an optic nerve. The cells of the distal layer have each a comb-like margin, and the proximal visual cells bear rods

with an axial neurofibril. The retina is of the inverted type. The eyes are not cephalic, but occur on the mantle-lobes.

There is no ground whatever for placing the Pecten eye in the same class as the vertebrate eye, for the resemblance is very superficial, and though the retina is inverted in both cases this has been produced in very different ways. If we consider Bütschli's observations as correct the retina of the Pecten eye has been formed from an invagination of the ectoderm, which forms a closed vesicle cut off from the surface. The distal wall of this gives rise to the retina, and the proximal to the pigment layer.

Amongst invertebrate eyes that of Spondylus is the only one that can be safely homologised with the Pecten eye. The structure of these organs is identical but for one point, a layer of cells in Spondylus takes the place of the non-cellular septum of the Pecten eye. The eye of Cardium can also be homologised, though with less certainty. There is a cellular lens, an inverted retina with two series of recipient cells, and also layers corresponding in position to the tapetum and pigment layer of Pecten. There is, however, another layer (the choroid) interpolated between the retina and tapetum, which may be taken as equivalent to the interstitial cells of the Pecten eye.

These are, so far as I am aware, the only vesicular eyes occurring in the Lamellibranchiata.

In the highly organised cephalopod eye we do not meet any resemblance to the Pecten eye, except that the visual cells bear rods with an axial neurofibril like these recipient structures in the latter. There is a single layer of recipient cells directed towards the light, and the lens is not cellular and arises quite differently from the lens of the arthropod eyes.

Amongst the Polychæta there are some highly organised visual organs, in particular those of the Alciopina, ex. Alciopa and Vanadis, and the large and complex organs of these forms have been studied in detail by Greeff and Hesse. The eye takes the form of a closed vesicle as in Pecten, the free pole being formed by a cellular cornea, a continuation of the

general epithelium of the body-wall. The inner wall of this optic vesicle is, however, also made up of a layer of cells, which though forming a complete hollow sphere, are differentiated in three regions, in structure and function. Those cells immediately under the cornea just spoken of are low and form a second and inner cornea. The cells lining the proximal half of the optic vesicle are the retinal cells, and between this area and the inner cornea the cells are again different and contain pigment.

There is only one series of recipient cells in the retina, and they bear rods which resemble those of the Pecten eye and contain a very distinct axial neurofibril. They are, however, directed towards the lens, that is, not inverted. The lens is spherical and non-cellular, and another difference from the eye of Pecten is produced by the presence of a vitreous body between lens and retina.

There are several interesting arthropod eyes that may be briefly referred to. The ocelli of Cloëon (one of the May-flies) are distinctly peculiar and are superficially rather like the Pecten eye, but this resemblance is due to the dioptric part of the eye, and not to the retina. We have again a closed vesicle. The cuticle extends over the cornea, but remains thin and does not form a corneal lens. The hypodermis forms a cornea similar to that of Pecten. Under this cornea and lying in the optic vesicle is a cellular lens strikingly like that of Pecten and altogether unlike other arthropod eyes. The retina is made up of two layers of cells, but the distal ones are not visual and the proximal ones forming the retina proper are not inverted.

Another interesting arthropod eye is the ocellus of Agrion. This bears some resemblance to the Pecten eye in the fact that there are two series of recipient cells in the retina. They are, however, not inverted. The distal part of the optic vesicle is quite different, and the chitinous exoskeleton or cuticle is thickened over the free surface, forming a corneal lens. This is a monomeniscous arthropod eye therefore, and the arrangement of the retinal cells is interesting.

The distal layer of sense-cells lie touching the lens, almost like the outer cells of Pecten touch the septum.

A striking difference from the Pecten retina is, however, present which lends at the same time support to the view of Leydig, upheld by Lankester in 1883, namely that the compound eye is formed by the segregation of the elements of a simple eye, and this is the segregation of the retinal cells. The visual cells do not remain, as in the Pecten eye, altogether independent with their recipient ends directed towards or away from the lens, but bear a comb-like margin of neurofibril endings laterally and are collected in groups of threes, each group being a retinula. Thus we have a monomeniscous eye with a retinulate retina, the whole being very different from the Pecten retina except in the one point —the presence of visual cells arranged in two layers.

The central eyes of the Scorpions may finally be mentioned here. These are also monomeniscous and present a far greater resemblance to the Pecten eye than appears at first sight. They are vesicular, though the cavity of the vesicle has disappeared and the retina is inverted, though, owing to a secondary reversion during development, this is not obvious.

The eyes are developed from an involution of the hypodermis or ectoderm, which, however, does not lie vertical to the surface. The outer wall becomes thickened and forms the retina; the inner wall remains thin and represents the post-retinal layer of ectoderm cells in the adult. This is strikingly like the process in the Pecten eye where the inner wall becomes the pigment layer. The retinal cells are of course inverted. The nerve-fibres are attached to the outer ends of these cells in the embryo, but, owing to reversion in the course of development, become connected to the inner ends in the adult eye. In the course of these changes the optic nerve must penetrate the post-retinal layer, and this has been shown by Ray Lankester and Bourne (**46**) to be the condition actually prevailing in the adult. Beyond this remarkable similarity in development the eyes

are very different: there is a retinulate retina of one layer of recipient cells which are segregated in groups of fives, and the dioptric part is again represented by a corneal lens.

It will be seen, therefore, that no eye outside the Lamellibranch group presents anything but isolated features of resemblance, and the only common structures appear to be the general occurrence of rods with axial neurofibrillæ or visual cells with a margin of cilia-like processes arranged like the teeth of a very fine comb, and these margins may form rhabdomes.

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EXPLANATION OF PLATES 6 AND 7,

Illustrating Mr. W. J. Dakin's paper on "The Eye of Pecten."

List of Reference Letters.

Ax. f. Axial fibril of rods. *B. m.* Basement-membrane. *Circ. n.* Circumpallial nerve. *Cent.* Centrosome of lens-cells. *Co.* Cornea. *Co. S.* Sub-corneal connective tissue. *Con.* Connective tissue of eye-stalk. *Cut.* Cuticle. *D. S.* Distal sense-cells. *D. Sn.* Nuclei of distal sense-cells. *Eye.* Eye. *I. I. C.* Inner interstitial cells. *L.* Lens. *L. C.* Lens-cells. *Lac.* Blood lacunæ of eye-stalk. *L. f.* Muscle-fibres on distal surface of lens. *M.* Mantle. *M. f.* Muscle-fibres of connective tissue of optic vesicle. *M. lf.* Muscle-fibres of lens surface. *Mus.*

Muscles of eye-stalk. *M. Ret.* Marginal area of retina. *N. Lf.* Nuclei of muscle-fibres of lens surface. *nuc.* Nucleus. *O. I. c.* Outer interstitial cells. *Op. D.* Distal branch optic nerve. *Op. Ds.* Sheath of distal nerve. *Op. N.* Optic nerve. *Op. P.* Proximal branch optic nerve. *Op. P*[11]. Fibres (separated) of proximal branch of optic nerve. *P. man.* Pigment-mantle. *Pg.* Pigment-layer. *R. C.* Rod-cells. *R. C. n.* Nuclei of rod-cells. *R. mat.* Rod-matrix. *Rod.* Rod. *S. m.* Pseudo sieve-membrane (see text). *Sc.* Modified connective-tissue wall of optic vesicle. *Sep.* Septum. *Ta.* Tapetum. *ta. c.* Pigment layer concretion. *V.* Velum.

PLATE 6.

Fig. 1.—Section through eye-stalk and eye, P. maximus. in a plane at right angles to that of the mantle surface; the right side of the figure represents the shell side of the eye. The various parts, lens, retina, etc., have been drawn with the camera lucida, but from different preparations, each showing best the part drawn. × 270.

PLATE 7.

Fig. 2.—Diagrammatic section through both mantle-lobes of P. jacobæus, illustrating the course of the nerves and difference in size of the eyes. The left mantle-lobe is to the left in the figure.

Fig. 3.—Upper surface of cornea, P. maximus. × 1000.

Fig. 4.—Transverse section of corneal cells at about the middle of their height. P. maximus. × 1000.

Fig. 5.—Isolated cells from the lens. P. maximus, maceration in chloral hydrate solution. × 570.

Fig. 6.—Lens-cells as seen in sections. *b.* Normal cells from Hermann-sublimate fixed specimen, P. varius. *a.* Cell from same specimen with large nucleus. Stain iron hæmatoxylin. *d.* Cell from lens fixed in von Rath's fluid. × 660.

Fig. 7.—Transverse section cutting layer of fibres between lens and subcorneal tissue. The fibres and cells are stained red with Mallory's connective-tissue stain, the subcorneal tissue blue. P. tenuicostatus. × 310.

Fig. 8.—Fibres between lens and subcorneal tissue; attached to the latter in a maceration preparation (chromic acid). P. jacobæus. × 300.

Fig. 9.—Cells and nuclei between lens and subcorneal tissue, as seen through the cornea, which has been teased from an eye fixed in Zenker's fluid. Iron hæmatoxylin. P. maximus. × 330.

Fig. 10.—Transverse section of cornea and subcorneal tissue of P. jacobæus (Bielschowsky-Paton method). × 650.

Fig. 11.—Isolated cells from distal surface of lens. P. maximus, chromic acid maceration. × 330.

Fig. 12.—Transverse section of cornea and pigment-mantle of P. tigrinus. Fixed Zenker, stained Mallory. × 300.

Fig. 13.—Schematic view of retinal elements, reconstructed from sections and macerations. The two left-hand rod-cells are shown in external view, from macerations, and the two right-hand ones in section. × about 920.

Fig. 13*a*.—Distal ends of two rod-cells (chromic acid maceration).

Fig. 14.—Rod-cells with partly broken-up rods, showing the bristle-like appearance of axial fibre. P. maximus (chromic acid maceration). × 900.

Fig. 15.—Isolated interstitial supporting cells from retina; *a* and *b* are two outer interstitial cells. P. maximus. Chromic acid and chloral hydrate macerations. × 900.

Fig. 16.—Transverse section of distal sense-cells and outer interstitial cells. Mallory's connective-tissue stain. P. maximus. × 940.

Fig. 17.—Transverse section of rods and rod-matrix. P. jacobæus. Fixed Zenker, stained by modified Weigert method. × 800.

Fig. 18.—Distal branch of optic nerve, breaking up into branches on surface of septum. P. jacobæus. From teased preparations. × 250.

Fig. 19.—Tapetum in surface view. From sections. The large circle shows relative size of a rod-cell in section. × 1600.